SEABIRD HABITAT USE AND ZOOPLANKTON ABUNDANCE AND BIOMASS IN RELATION TO WATER MASS PROPERTIES IN THE NORTHERN GULF OF ALASKA

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A

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ABSTRACT

Understanding of biological and physical mechanisms that control the Gulf of Alaska (GOA) ecosystem is of major importance to predicting the responses of bird and zooplankton communities to environmental changes in this region. I investigated seasonal (March-October) changes in seabird abundance in relation to changes in zooplankton biomass and water mass properties from 1998 to 2003. *Oceanodroma furcata* and *Fratercula cirrhata* were most abundant during the peak of the zooplankton production season (May-August). Overall abundance of seabirds did not follow seasonal changes in zooplankton biomass. Seabird abundance was low in the study area when compared to other regions in the GOA. Furthermore, low bird densities suggest that productivity in this study area is not high enough to sustain a significant seasonal increase in local seabird abundance.

I further investigated the distribution and abundance of seabird foraging guilds across the neritic and oceanic domains in relation to water mass properties and zooplankton biomass during March and April. Overall zooplankton biomass increased from the inner shelf to the oceanic domain. Highest density of subsurface-foraging seabirds occurred in the middle shelf and surface-feeding seabirds were most abundant in the middle shelf and oceanic domain. Murre (*Uria* spp.) abundance was positively correlated with the biomass of *Thysanoessa inermis*, and Northern Fulmars (*Fulmarus glacialis)* were associated with cephalopod paralarvae and *Eucalanus bungii*. Elevated

biomass of *Thysanoessa inermis* in March and April may be an important factor influencing habitat choice of wintering murres in this region.

Lastly, I investigated the inter-annual variation in the abundance of sixteen zooplankton taxa in relation to water mass properties during May from 1998 to 2009. Significant variations in temperature, salinity and zooplankton abundance were identified. *Thysanoessa inermis* and *Calanus marshallae* had increased abundances in years when there was a strong phytoplankton spring bloom preceded by anomalously cold winters. However, abundances of *Pseudocalanus* spp., *Neocalanus plumchrus/Neocalanus flemingeri*, *Euphausia pacifica* and *Oithona* spp. were not strongly affected by relatively higher mean water temperatures. The abundance of zooplankton in the northern GOA was highly influenced by advective processes.

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INTRODUCTION

The Gulf of Alaska (GOA) has a rich and diverse ecosystem, which sustains a number of important fisheries resources and approximately 8 million nesting seabirds (Ware and McFarlane 1989; Springer et al. 1999; Weingartner et al. 2002)[1]. The top predators in this ecosystem depend on the seasonal increase in primary and secondary productivity and have their life cycles timed so that their offspring may benefit from the seasonal abundance in food resources (Coyle and Pinchuk 2003; Childers et al. 2005; Williams et al. 2008; Breton et al. 2009). Nevertheless, the magnitude of the seasonal increase in productivity is subject to spatial and temporal variability. This study investigated the temporal and spatial variations of top predators (seabirds) and secondary producers (zooplankton) in relation to water mass properties in the northern GOA (59.8450° N and 149.4667° W to 58.0983° N and 147.7933° W).

Seabirds

A wide variety of seabird foraging guilds occurs in the GOA, which include: surface feeders, surface plungers, divers and kleptoparasitic birds (Ashmole 1971; Gould et al. 1982; Wahl et al. 1989). During the breeding season adult seabirds become aggregated near shore due to nest attendance, and during the non-breeding season they

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[1] The citations for this introduction are listed in the reference section for this dissertation on page 185

are able to disperse (Gould et al. 1982; Hunt et al. 2005; Day 2006). Resident species of seabirds remain in the northern GOA after the breeding season and need to acclimate to a decrease in prey abundance. During this period, resident species have to search for prey in an environment where contrast between high and low density prey patches is low and therefore more difficult to detect. Nevertheless, neritic and oceanic zones remain intrinsic components of the marine habitat.

Seabirds are not equally distributed throughout the world's oceans. Factors such as food availability, morphological and physiological adaptations, life history, predation avoidance, and the physical environment contribute to their differential distribution across varying temporal and spatial scales (Hunt and Schneider 1987; Schreiber and Burger 2002). At large spatial scales (1000's km) patterns in primary production triggered by physical forcing appear to drive the distribution of seabirds. Polar and sub polar regions like the GOA are highly productive with distinct phytoplankton and zooplankton communities sustaining upper trophic levels such as juvenile and adult fishes, seabirds and marine mammals (Mann and Lazier 1996; Springer et al. 1996; Mackas and Tsuda 1999). High productivity over a large scale allows migratory and resident species to exploit the GOA shelf environment and maintain high abundances. However, high productivity areas in the meso-scale are not as predictable when compared to large scales (Fauchald et al. 2002; Vilchis et al. 2006). This is partly explained by the higher variability in physical processes such as upwelling, changes in thermocline depth, eddy activity and freshwater discharge, all of which influence the distribution of marine

resources (Nel et al. 2001; Hyrenbach and Veit 2003; Okkonen et al. 2003; Coyle and Pinchuk 2005; Weingartner et al. 2005). In addition, factors such as the schooling behavior of fishes and diel vertical migration of zooplankton contribute to the difficulty in predicting the distribution of seabirds and their prey (Pahlke 1985; Hanamura et al. 1989).

The distribution and abundance of highly mobile marine predators such as seabirds are most probably determined by physical processes and lower trophic level interactions at large and meso scales, while individual seabird behavior influences their distribution patterns at small scales. However, these relationships are not static and new patterns in distribution and abundance may emerge in a changing environment.

Physical environment

The GOA is a semi-enclosed basin in the North Pacific and two current systems dominate its circulation: the Subarctic Gyre in the ocean basin, and the Alaska Coastal Current (ACC) on the continental shelf (Stabeno et al. 2004). The ACC is driven by wind and buoyancy, and originates on the British Columbia shelf; the ACC flows northward along the inner shelf and through passages in southeast Alaska, then westward along the south coast of Alaska, before entering the Bering Sea through Unimak Pass and Samalga Pass in the western gulf (Schumacher et al. 1982; Schumacher et al. 1989). The southern boundary of the Subarctic Gyre is the North Pacific Current; as it approaches the west coast of North America it bifurcates into the southward-flowing California Current

and the northward-flowing Alaska Current. The Alaska Current is an eastern boundary current, rich in eddies and meanders (Okkonen et al. 2003; Janout et al. 2009). In the northern GOA the Alaska Current turns southwestward, following the isobaths, and narrows and intensifies to become the Alaskan Stream, a western boundary current of the Subarctic Gyre. West of Kodiak Island, the Alaskan Stream is a narrow (~50 km wide), high speed (>50 cm s^{-1}) current that flows southwestward along the slope of the Alaska Peninsula and the Aleutian Islands (Reed 1984; Reed and Stabeno 1989).

The GOA is under intense atmospheric forcing by the Aleutian Low, especially during the winter months (November-March). The intensity and frequency of storms that comprise the Aleutian Low vary seasonally because of the variations in low-pressure formation and the influence of the Siberian and East Pacific high pressure systems (Wilson and Overland 1986). Throughout late spring and summer the East Pacific High strengthens and moves northward, while the Aleutian Low and the Siberian High weaken. In fall and winter the Aleutian Low "deepens" and moves westward, the East Pacific High weakens and moves southward offshore of California, and polar air masses accumulate over northeast Siberia, strengthening the Siberian High pressure system (Weingartner et al. 2005). The strong horizontal pressure gradient between these air masses generates a cyclonic flow, northeastward in the southeast region and southwestward in the northwest region of the Aleutian Low. As the warm, moist air rises upon encountering the mountainous Pacific Coast, it cools, leading to increased cloud cover and high precipitation. In the western region of the Aleutian Low precipitation is

lower because the air is cooler and most of the precipitation has taken place over the Gulf of Alaska.

Zooplankton and hydrography

The zooplankton community in the GOA is mainly composed of copepods, euphausiids, chaetognaths, pteropods, salps and medusae. The biomass in the zooplankton community is usually dominated by large oceanic copepods, such as *Neocalanus cristatus, N. plumchrus, N. flemingeri* and *Eucalanus bungii*, which are responsible for the annual biomass peak during spring and early summer (Coyle and Pinchuk 2003). This seasonal biomass peak is related to life cycle timing of these dominant copepod species, which over-winter in deep waters and migrate above the pycnocline in spring and early summer to feed and complete their somatic growth (Miller and Clemons 1988; Tsuda et al. 1999; Kobari and Ikeda 2001). Subsequently, the rapid summer decline in biomass occurs mainly because these four species migrate to diapause in deep waters. On the other hand, small neritic copepods, such as *Calanus marshallae, Metridia pacifica, Pseudocalanus* spp. and *Oithona* spp., are the most populous species in the zooplankton community, which has an overall annual abundance peak during summer (Coyle and Pinchuk 2003). Later, during winter, overall mesozooplankton biomass and abundance are at their lowest (Goldblatt et al. 1999). Therefore, the biomass and abundance peaks in zooplankton species in the GOA are mainly represented by oceanic and neritic copepod species, respectively.

Spatial patterns in distribution and abundance of zooplankton in the GOA are not only a result of their behavior and life history but are also a response to the coupling of physical and biological processes. In the northern GOA, during winter (December-February), the Aleutian Low is strong and along-shelf winds force an onshore Ekman transport of surface waters and downwelling near the coast. At this time of year the water column is nearly isothermal and the ACC front lies ~10 km off the coast, and most of the salinity gradient across the shelf occurs in the front, which extends from surface to bottom (Weingartner et al. 2005). During winter strong winds promote vertical mixing, which replenishes nutrients to the upper water column. However, the intense mixing prevents stratification of the water column. In addition, phytoplankton receive little insolation during this period, and chlorophyll *a* concentrations are low (Childers et al. 2005); therefore, biological production is low in the winter season. Furthermore, zooplankton biomass and abundance are at their lowest and they are distributed across the shelf.

The increase in short-wave radiation and freshwater runoff in conjunction with the decrease in wind speed as the Aleutian Low weakens, triggers stratification during spring (March-May). Given these conditions, surface water temperature starts to increase while salinity begins to decrease, leading to an increase in stratification and therefore water-column stability (Weingartner et al. 2005). When the water column is stable enough to prevent vertical mixing deeper than the critical depth, the spring bloom commences. As the spring bloom develops, chlorophyll *a* concentrations increase in the

upper water column (~20 m) and nutrient concentrations (nitrate, silicate and phosphate) decrease, indicating an increase in primary production (Childers et al. 2005). Concurrently, *N. plumchrus, N. flemingeri, N. cristatus* and *E. bungii* return from their winter diapause in deep waters and are distributed above the permanent pycnocline (~150 m) where they feed, grow and dominate the zooplankton biomass (Mackas and Tsuda 1999).

The development of the spring bloom is not uniform across the GOA shelf. Stratification occurs first in the inner shelf, bays and fjords because coastal freshwater runoff is restricted to near-shore regions and slowly extends offshore through ocean advection and horizontal mixing processes. Thermal stratification depends on surface heating and wind mixing, and occurs later in the mid-shelf, slope and the outer shelf regions (Weingartner et al. 2005). During summer (June-August), a strong thermocline (~25 m depth) and vertical density gradient develops across the shelf but cross-shelf salinity gradients are weak. At this time the ACC front extends farther offshore (~40-50 km) and is ~ < 40 m deep. These changes in vertical and horizontal stratification influence the circulation across the GOA shelf, especially because of wind relaxation and the "shallowing" of the ACC and the shelf-break front. Weak upwelling occurs on the inshore side and at the base of the shelf-break front. In addition, there is an onshore flow at the bottom associated with shoreward movement of the base of this front (Weingartner et al. 2005). During fall (September-November), freshwater discharge is highest. Along-shelf winds and coastal downwelling increase and the ACC front moves shoreward to

within ~30 km of the coast, intersecting the bottom between 50 and 100 m (Weingartner et al. 2005). Furthermore, zooplankton abundance and biomass decline, and differences in their cross-shelf distribution are minimized (Coyle and Pinchuk 2005).

Seabirds, zooplankton and hydrography

Given the seasonal increase (May-August) in primary and secondary productivity, and in seabird abundance at large scales in the GOA (Gould et al. 1982; Mackas and Coyle 2005; Whitney et al. 2005), it was of interest to investgate if these changes occurred at a meso-scale in the northern GOA and if patterns in seabird abundance were associated with seasonal changes in zooplankton biomass and water column properties. This rationale is based on the fact that zooplankton are the primary prey for forage fish and small cephalopods (Brodeur and Wilson 1996; Wilson et al. 2006; Jorgensen 2007), which in turn are major prey resources for seabirds (Springer et al. 1996; Hunt et al. 1998; Rowe et al. 2000; Davoren et al. 2003; Garthe et al. 2004). There is a lag in time (weeks) among peaks of zooplankton biomass, fish abundance and birds which cannot be ignored when studing associations between seabirds and their potential prey. However, this lag time becomes less important when investigating these associations at large temporal (years) and spatial (1000's) scales (Valiela 1995; Mann and Lazier 1996; Schneider 1994). The importance of this study lies on the fact that, if seasonal changes in seabird abundance are similar in large and meso scales to those observed in zooplankton biomass and water mass properties (Stabeno et al. 2004; Coyle

and Pinchuk 2005; Mackas and Coyle 2005; Weingartner et al. 2005; Whitney et al. 2005), then they can be used to explain and/or predict seasonal variations in seabird distribution and abundance. If the opposite is true, then these may not be the best parameters to understand meso-scale seasonal variations in seabird abundance in the northern GOA.

Spatial variability in water mass and zooplankton distribution is also large in the northern GOA, in addition to the aforementioned seasonal changes (Coyle and Pinchuk 2005; Weingartner et al. 2005). These parameters characterize neritic and oceanic habitats and their spatial variability may play an important role in habitat choice of seabird foraging guilds (Ainley 1977; Wahl et al. 1989). Therefore, if the distribution and abundance of seabird foraging guilds are found to be associated with spatial variations of neritic and oceanic water masses and zooplankton species, then these parameters may be more useful in characterizing oceanic and neritic habitat use of seabirds than the static bathymetry features such as continental shelf slope isobaths that have been used to delineate these environments (Yen et al. 2005; O'Hara et al. 2006).

Zooplankton species may respond differently to changes in temperature and food concentration, and their abundance may also change as a result of vertical and cross-shelf mixing that may affect dispersal of organisms in the water column (Coyle and Pinchuk 2005; Mackas and Coyle 2005; Pinchuk et al. 2008). Therefore, it is important to understand how zooplankton species respond to changes in water mass properties. Effects of an El Nino event (1997-1998) followed by a La Nina event (1998-1999), and

cooler winter temperatures in 2001-2002 and 2006-2009 have been reported for the northern GOA (Weingartner et al. 2005; Janout et al. 2010). Furthermore, a multi-year (1998-2009) data set of water mass properties and zooplankton net samples collected during the month of May has been built for the northern GOA. Given this opportunity, it was of interest to this study to investigate associations between zooplankton abundance and inter-annual changes in water mass properties in the northern GOA. If these associations are detected, then changes in the zooplankton community can be predicted in relation to climate variabiltiy.

In summary, this study focuses on seasonal changes in seabird abundance and distribution in relation to zooplankton biomass and water mass properties in the northern GOA from 1998-2003. In addition, habitat use of neritic and oceanic domains by seabird foraging guilds is characterized during winter and early spring, in relation to zooplankton biomass and water mass properties, in the northern GOA. Finally, this study identifies inter-annual changes in zooplankton abundance and community composition in relation to water mass properties in the northern GOA during May from 1998 to 2009.

CHAPTER 1. Seasonal characterization of seabird distribution and habitat use in the northern Gulf of Alaska[2]

Abstract

Seabird studies in the Gulf of Alaska (GOA) have been mostly limited to coastal regions and to the breeding season. Little is known of the response of seabird populations to seasonal changes in forage. I therefore examined the hypothesis that seabird pelagic abundance follows the increase and decrease in zooplankton biomass in the subarctic throughout its complete seasonal cycle. Research cruises were conducted in March, April, May, July, August, October and December from 1997-2003, in the northern GOA. Monthly means of seabird abundance were calculated in addition to zooplankton biomass, temperature and salinity. Fork-tailed storm petrels (*Oceanodroma furcata*), northern fulmars (*Fulmarus glacialis*) and common murres (*Uria aalge*) were the most abundant avian species. Gulls (*Larus* spp. and *Rissa tridacytila*) represented only nine percent of seabirds and dark shearwaters were not a dominant species group. Overall abundance of seabirds did not follow seasonal changes in zooplankton biomass. Fork-tailed storm-petrels and tufted puffins (*Fratercula cirrhata*) were most abundant during the peak of the production season (May-August) and northern fulmar abundance did not change with season. The results of this project suggest that productivity in the

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[2] Sousa L., Day R., Coyle K., Weingartner T., (2011) Seasonal characterization of seabird distribution and habitat use in the northern Gulf of Alaska. Prepared for submission in *Marine Biology*

study area is not enough to sustain a significant seasonal increase in local seabird abundance.

Keywords: seabird abundance, zooplankton biomass, salinity, temperature

Introduction

The majority of seabird studies in the northern GOA have been spatially restricted to the coastal region and temporally concentrated on the breeding season (May-August) (Hatch and Sanger 1992; Springer et al. 1999; Ainley et al. 2003; Harding et al. 2007). Little seabird research has been conducted across the continental shelf into the oceanic domain during winter months (Gould et al. 1982; Harrison 1982; Day 2006). As a result, there is a lack of seasonal and inter-annual coverage of cross-shelf distributions of seabirds in this region. The purpose of this study was to obtain a comprehensive view of the seasonal changes in seabird habitat and distribution, and to determine if seabird abundance follows the seasonal changes in zooplankton biomass in a subarctic marine ecosystem. The latter objective is based on the fact that zooplankton are the primary prey for forage fish and small cephalopods (Brodeur and Wilson 1996; Wilson et al. 2006; Jorgensen 2007), which in turn are major prey resources for seabirds (Springer et al. 1996; Hunt et al. 1998; Rowe et al. 2000; Davoren et al. 2003; Garthe et al. 2004). Therefore, to achieve this objective, data were collected on seabird abundance, zooplankton biomass and water column properties across the shelf of the northern GOA during winter, spring, summer, and fall from 1997-2003. The results of this study include

six years of data that encompass the complete seasonal cycle of the water column and the changes in seabird species composition and abundance.

The GOA supports approximately 8 million nesting seabirds (Springer et al. 1999; Stephensen and Irons 2003). Seabird abundance is highest during the breeding season and ranges from 29 birds km^{-2} in spring to 8 birds km^{-2} in summer, and lowest during the non-breeding season with abundances decreasing to 3 birds km^{-2} in the fall to < 1 bird km^{-2} in winter (Springer et al. 1999). However, the northern GOA has lower seasonal variations in seabird abundance than the GOA in its entirety (Hunt et al. 2005). As the breeding season progresses, migrating birds contribute to an increase in the GOA seabird diversity and abundance, and resident bird species become more aggregated near shore (Gould et al. 1982). In summer, breeding adults become central place foragers (Orians and Pearson 1979) restricted to the vicinity of their breeding colonies, and are further constrained by high energetic costs of long-distance flights and diving (Houston et al. 1996). Therefore, seabirds have their home range restricted by patterns of colony attendance during the breeding season, but are relieved of these restrictions, and able to disperse, during the non-breeding season.

The GOA shelf waters are characterized by two major currents, the Alaska Current, which flows westward at or near the shelf break, and the Alaska coastal current (ACC), which flows westward within 20–50 km of the shore line (Figure 1.1) (Royer 1982; Weingartner et al. 2005). The Alaska Current offshore Kodiak Island narrows and intensifies to become the Alaskan Stream, a western boundary current of the Subarctic

Gyre. West of Kodiak Island, the Alaskan Stream is a narrow (~50 km), high speed (>50 cm s^{-1}) current that flows southwestward along the slope of the Alaska Peninsula and the Aleutian Islands (Reed 1984; Reed and Stabeno 1989). The ACC is driven by wind and buoyancy, and originates on the British Columbia shelf; the ACC flows northward along the inner shelf and through passages in southeast Alaska, then westward along the south coast of Alaska, before entering the Bering Sea through Unimak Pass and Samalga Pass in the western Gulf (Schumacher et al. 1982; Schumacher et al. 1989).

The zooplankton community in the northern GOA is mainly composed of calanoid copepods, euphausiids, chaetognaths and cnidarians (Coyle and Pinchuk 2003). Biomass in the zooplankton community during spring and early summer is usually dominated by large oceanic copepods, such as *Neocalanus cristatus*, *N. plumchrus*, and *N. flemingeri,* which are responsible for the annual biomass peak (Coyle and Pinchuk 2003). This seasonal biomass peak is related to the life cycle of these dominant copepod species, which over-winter in deep waters and migrate above the pycnocline in spring and early summer to feed and complete their somatic growth (Miller and Clemons 1988). Subsequently, a rapid summer decline in biomass in the upper 100 m occurs mainly because these three species migrate to diapause in deep waters (Coyle and Pinchuk 2005). However, smaller neritic copepods, such as *Calanus marshallae*, *Metridia pacifica*, *Pseudocalanus* spp. and *Oithona* spp., are the most populous species in the zooplankton community, which have their annual abundance peak in summer (Coyle and Pinchuk 2003). In winter, overall mesozooplankton biomass and abundance are at their lowest

(Goldblatt et al. 1999). Therefore, the biomass and abundance peaks in zooplankton species in the GOA are mainly represented by oceanic and neritic copepod species, respectively.

This study presents information on the abundance of seabirds in the northern GOA during the breeding and non-breeding seasons in relation to seasonal changes in water mass properties, chlorophyll *a* concentration, and zooplankton biomass across the coastal and oceanic domains over a 6-year period (1997-2003).

Methods

Seabirds

As part of the Global Ocean Ecosystems Dynamics (GLOBEC) Long Term Observation Program (LTOP) in the northern GOA, surveys were conducted along the Seward line (~220 km) during March, April, May, July, August, October and December from 1997 to 2003 (Figure 1.2; Table 1.1). Seabirds were continuously counted during daylight hours (enough light for acceptable visibility), within a 300 m wide transect at a 90 ° angle from bow of the ship to its starboard side (Tasker et al. 1984). Birds were observed with the naked eye and with the aid of binoculars (10 x 42) from the bridge of the RV *Alpha Helix* (eye height = 7.7 m above sea surface), which cruised at ~18 km/h. At the beginning of each count interval, the ship's position, speed, Beaufort scale, and observational conditions were recorded (Appendix 1). A new count interval was initiated

every five minutes following the previous count. Birds sighted within the survey strip were counted and identified to the lowest possible taxonomic level. Their positions and behaviors (sitting, feeding and flying) were also recorded on a portable computer. Birds that approached the ship from behind were considered to be ship followers and were recorded only once and then ignored. Flying birds were counted using the "snapshot method" to prevent overestimation of seabird densities caused by the movement of flying birds through the transect (Tasker et al. 1984; Gould and Forsell 1989). The "snapshop method" consists of counting birds only once, by scanning the survey area at the beginning of each count interval (Tasker et al. 1984; Gould and Forsell 1989). Birds on the water were counted continuously because they are more difficult to detect with one scan. Flight direction of seabirds in relation to the course of the ship (Spear et al. 1992) was not accounted for during the surveys, and as a result there is not an estimate of absolute bird densities but rather an index of relative bird density. In this study, bird counts per km^{-2} are considered to be an index of relative abundance and are hereafter referred to as seabird abundance.

Analyses included all birds, regardless of behavior, sighted along transects. A total of 3004 km^2 of ocean surface was scanned throughout ~ 580 hours of effort during 33 cruises conducted between 1997 and 2003 (Table 1). Monthly density of seabirds was calculated as follows:

$$X = \frac{\left(\frac{count_1}{area_1}\right) + \left(\frac{count_2}{area_2}\right) + \ldots + \left(\frac{count_n}{area_n}\right)}{n} \qquad \text{(Equation 1.1)}$$

where X is the mean monthly density of seabirds, *count* is the bird count for each cruise, *area* is the area surveyed in each cruise in km^2, and n is the number of cruises in each month. Using the total area surveyed to calculate bird densities per cruise, allowed me to account for the difference in total ocean surface scanned for each month, when calculating mean monthly densities.

Seabird species were divided into categories according to the most abundant taxa during this study to provide a more robust analysis of the seabird community throughout the seasons. Species that were rarely observed in transects and/or that represented less than 5% of the seabird community and of major taxa, were not included in the statistical analyses and are referred to as "others". Marbled murrelets (*Brachyramphus marmoratus*), Kittlitz's murrelets (*Brachyramphus brevirostris*), unidentified murrelets (*Brachyramphus* spp.), and ancient murrelets (*Synthliboramphus antiquus*) were combined into one species category (murrelets) because together they comprised 8% of Alcidae but individually they did not represent more than 2% of Alcidae. In addition, over 25% of murrelets could only be identified to the genus level (*Brachyramphus spp.*). Puffins (tufted puffins-*Fratercula cirrhata* and horned puffins-*Fratercula corniculata*), and terns (Arctic tern-*Sterna paradisaea*, Aleutian tern-*Sterna aleutica*) were combined into the "puffin" and "tern"categories, respectively, because of their similar diets and foraging strategies and because horned puffins and Aleutian terns did not represent more

than 2% and 0.5% of Alcidae and Laridae, respectively. Occasionally it was not possible to distinguish between common murres (*Uria aalge*) and thick-billed murres (*Uria lomvia*), sooty shearwaters (*Puffinus griseus*) and short-tailed shearwaters (*Puffinus tenuirostris*), fork-tailed storm-petrels (*Oceanodroma furcata*) and Leach's storm-petrels (*Oceanodroma leucorhoa*). Therefore, observations of these species were combined into three categories: murres (*Uria* spp.), dark shearwaters (*Puffinus* spp.), and storm-petrels (*Oceanodroma* spp.). Of all murres and storm-petrels identified to the species level, 99% were common murres and 95% were fork-tailed storm-petrels, respectively. The species categories used in the analyses are listed in Table 2, and Appendix 2 contains a complete list of all species counts for this study.

Seasonality

Seasons were defined based on the intensity of cyclonic winds and the amount of fresh water discharge in the study area (Weingartner et al. 2005). Winter (November–March) is characterized by very intense cyclonic winds that begin to weaken in the spring (April–May) and are at their lowest speeds in summer months (June-September), whereas the fall (October) can be characterized by the highest amount of freshwater discharge coupled with an increase in cyclonic wind strength (Figure 1.3a). Breeding and non-breeding seasons for the observed seabird species were defined based on the information in Birds of North America (Figure 1.3b) (Poole 2005). Not all birds observed during the

breeding season were in fact breeding, since these samples probably contained failed breeders and non-breeding birds.

Hydrography

Conductivity-temperature-depth (CTD) and fluorescence profiles were collected from surface to bottom depths at 1 m increments using a Seabird model 911 Plus fitted with conductivity, temperature and fluorescence sensors (Weingartner et al. 2005). Nineteen stations at ~8 km intervals were sampled along the shelf and slope, and three stations at ~18 km intervals were sampled off the shelf break (Figure 1.2). Mean temperature and salinity were calculated by averaging data collected from the upper 100 m. Pycnocline depths were determined by calculating the depth of greatest change in sigma-t through the water column. Upper and lower temperature and salinity were calculated by averaging the data from above and below the pycnocline to a maximum depth of 100 m.

Zooplankton

Zooplankton net samples were collected at night with a 1-m^{-2} Multiple Opening/ Closing Net and Environmental Sampling System (MOCNESS) (Wiebe et al. 1976) with 500 μm mesh nets. Zooplankton samples were taken at 13 stations spaced 18 km apart along the Seward line (Figure 2) (Coyle and Pinchuk 2005). The nets were fished at night and five oblique samples were collected in 20-m increments from 100 m depth to

the surface. Samples were preserved in a 10% formalin seawater solution and stored for later analysis. All animals in the samples were sorted and identified to the lowest taxonomic category possible and wet-weight biomass estimates were calculated following the methods of Coyle and Pinchuk (2005). Zooplankton biomass was integrated from the upper 45 m of the water column because the majority of the zooplankton and seabird forage species are distributed within this depth range (Brodeur and Rugen 1994; Brodeur and Wilson 1996; Coyle and Pinchuk 2005), and the community in the upper 45 m depth is therefore considered to be representative of the organisms that may be available to foraging seabirds and their prey in the study area (Hatch and Nettleship 1998; Boersma and Silva 2001; Ainley et al. 2002; Hatch et al. 2009). Furthermore, the short-term temporal (hours) and spatial (meters) mis-match between zooplankton sampling (night-diel vertical migration of some species) and seabird surveys (day) are unlikely to influence the analysis of this study because of the large temporal and spatial scales covered (6 years and 3004 km^2).

Data analyses

The high heteroscedasticity, variability, overdispersion and zero-inflated data prevented the use of regression analysis, generalized additive models (GAMs) and generalized additive models for location scale and shape (GAMLSS) (Stasinopoulos and Rigby 2007) for the detection of linear or non-linear relationships between seabird abundance, zooplankton biomass and water column properties. Logarithmic

transformations and model adjustment using negative binomial distributions, or "quasi" link functions for zero-inflated and overdispersed data did not eliminate these problems (Venebles and Ripley 2002; Wood 2006). Therefore, non-parametric and parametric analysis of variance and multiple comparison methods were used to analyze the seabird and zooplankton data, respectively.

The data collected in this study were used to characterize seasonal changes in seabird abundance and habitat. We tested the alternative hypothesis that mean seabird abundance and mean zooplankton biomass are different between months, in opposition to the null hypothesis that mean seabird abundance and zooplankton biomass are not different between months. These hypotheses were developed to examine the relationship between seabird abundance and seasonal changes in zooplankton biomass in the northern GOA.

Non-parametric Kruskal-Wallis analysis of variance (from here on referred to as Kruskal-Wallis test) was used to test the alternative hypothesis that the mean abundance of seabirds was different between months ($n = 33$) (Zar 1999). Furthermore, non-parametric Nemenyi-Damico-Wolfe-Dunn joint ranking multiple comparison test (from here on referred to as NDWD test) was used to identify which months were significantly different (Hollander and Wolfe 1999; van de Wiel 2001), regarding the mean abundance of seabirds. Open-source statistical software R (R Development Core Team 2009) and the packages "coin" and "multcomp" were used for Kruskal-Wallis test and NDWD, respectively (Hothorn et al. 2006; Hothorn et al. 2008). Tests were considered significant

if $p \leq 0.05$. The NDWD test returns a global p-value which detects significant differences between pairs, and lists specific p-values for each pair-wise comparison (Hollander and Wolfe 1999; van de Wiel 2001). Because the NDWD test global p-value indicates differences between each data pair while the Kruskal-Wallis p-value indicates overall variance in the dataset, the two tests may produce discordant p-values, since they detect the variance in the data set at different levels of detail, so the tests are complimentary. The p-value of the NDWD test for each pair-wise comparison is computed via Monte-Carlo re-sampling and accounts for the probability of a cumulative Type I error.

Analysis of variance was used to test the alternative hypothesis that mean zooplankton biomass was different between months (n=34) (Zar 1999). The zooplankton analyses were performed using STATISTICA 6 software. The zooplankton biomass was power-transformed to stabilize the variance and results were considered significant if $p \leq 0.05$. Tukey's test was used to identify which months had significantly different mean zooplankton biomass. The significance level α in the Tukey test is the probability of encountering at least one Type I error during the comparison of all pairs of means, not the probability of committing a Type I error for a single comparison. Therefore, the Tukey test controls for probability of a cumulative Type I error.

Spearman correlation was used to detect linear trends between seabird abundance and zooplankton biomass. The biomass of Salpidae, Ctenophora and Cnidaria was

subtracted from the total biomass used in the correlation, because 90% of the biomass of these taxa is water, which can inflate the absolute total biomass for individual surveys.

Results

Seabirds

The majority of birds (56%) observed along the Seward line between 1997-2003 were tubenoses (Procellariiformes), followed by alcids (Alcidae) and gulls (Laridae), which comprised 30% and 9% of the total birds, respectively (Figure 1.4a). The remaining 5%, referred to as "others" in Figures 1.4a and 1.4b, were waterfowl (Anseriformes), loons (*Gavia* spp.), cormorants (*Phalacrocorax* spp.), jaegers (Stercorariidae), and phalaropes (*Phalaropus* spp.). Overall seabird abundance was not significantly different between months (Tables 1.2, 1.3), despite the apparent elevated seabird abundance in May (Figure 1.4b). Abundances of Alcidae and Procellariiformes were significantly different between months (Table 1.2). Procellariiformes abundance increased from March (mean = 1.325 birds km^{-2}, standard deviation ± 1.010 birds km^{-2}) through May (mean = 8.247 ± 7.521 birds km^{-2}) and decreased from May to December (mean = 2.585 ± 1.241 birds km^{-2}). However, only May and March abundances were significantly different (Figure 1.4b, Table 1.3). Alcid abundance was similar throughout all months with a mean of 2.156 ± 1.227 birds km^{-2} with the exception of October, when mean abundance was 0.551 ± 0.529 birds km^{-2} (Figure 1.4b, Table 1.3). Gull abundance

was significantly different among months according to the Kruskal-Wallis test (Table 1.2). However, the NDWD test did not detect significant differences in mean gull abundance between specific pair(s) of months (Tables 1.2, 1.3).

Storm-petrels (48%), northern fulmars (33%) and dark shearwaters (10%) comprised the majority of the Procellariiformes, while black-footed albatrosses (6%), Laysan albatrosses (2%) and other tubenoses (1%) composed less than 10% (Figure 1.5a). Storm-petrel, black-footed albatross and dark shearwater abundances were significantly different between months (Table 1.2). However, differences in dark shearwater abundance were only detected by the NDWD test. Storm-petrel abundance was greatest during breeding months (May and August) when compared to non-breeding months (October–April) (Figure 1.5b, Table 1.4) with mean abundances ranging from a low of 0.065 ± 0.048 birds km^{-2} in March to a high of 5.394 ± 7.605 birds km^{-2} in May. Dark shearwaters and black-footed albatrosses were more abundant in May and August-October, respectively, than in March (Figure 1.5b, Table 1.4). Northern fulmars were frequently present in the study area and their abundance varied little throughout the year, averaging 1.498 ± 1.278 birds km^{-2}. Storm-petrels were responsible for the seasonal variation in the abundance of Procellariiformes (Figure 1.5b).

Murres (61%) and puffins (30%) were the most abundant alcids (Figure 1.6a). Murre, puffin and murrelet abundance was significantly different between months (Table 1.2). However, differences in murrelet abundance were only detected by the Kruskal-Wallis test (Table 1.2). Murre abundance was lowest in October with mean densities of

0.288 ± 0.334 birds km^{-2}, which was significantly lower than March, April and December (Figure 1.6b, Table 1.5). Puffin abundance was highest during the breeding season (May-August) with densities of approximately 1.383 ± 0.518 birds km^{-2}; however, only spring abundance (May) was significantly higher than abundance in all non-breeding months (March, April and December) (Figure 1.6b, Table 1.5). Murres were the most abundant of all other Alcidae species groups during the non breeding winter months with mean densities of 2.443 ± 1.252 birds km^{-2}, and as puffin abundance increased during the spring and summer months murres no longer represented the majority of the Alcidae community (Figure 1.6b).

Black-legged kittiwakes (55%) and glaucous-winged gulls (33%) were the most abundant gulls (Figure 1.7a). Black-legged kittiwake abundance varied between months and there were significantly fewer in July and August when compared to March (Figure 1.7b, Tables 1.2, 1.6). Tern abundance was highest in May and August, which were the only months in which they were observed (Figure 1.7b, Tables 1.2, 1.6). Glaucous-winged gull abundance was significantly different between months according to the Kruskal-Wallis test. However, the NDWD test did not detect any specific pair(s) of months in which glaucous-winged gull abundances were significantly different (Tables 1.2, 1.6). Laridae species groups occurred in very low densities throughout the study period.

Zooplankton

Total zooplankton biomass peaked in May, with a mean total of 0.571 g m^{-3} (lower confidence interval (CI) = 0.487, upper CI = 0.667 g m^{-3}). Mean total zooplankton biomass was at its lowest levels in March (mean = 0.060, lower CI = 0.0476, upper CI = 0.076 g m^{-3}), while intermediate levels occurred in April, July, August, and October (Figure 1.8a). From the months that had intermediate values of mean total zooplankton biomass, only August differed significantly from April and October (Table 1.7). Crustaceans comprised 87% of the total zooplankton biomass, which consisted of 92% calanoid copepods (Figure 1.8b). Calanoida was the major zooplankton taxon contributing to the increase in total zooplankton biomass in May when they increased from ~0.100 g m^{-3} in April to ~0.450 g m^{-3} (Figure 1.8c).

Euphausiacea and Cnidaria biomass increased from July to October (Figures 1.8d, 1.8e, Table 1.7). Euphausiacea and Cnidaria had significantly higher biomass in the months of August and October. Chaetognatha biomass was highest from May to August (Figure 1.8f, Table 1.7). As total zooplankton mean biomass decreased between July and October, the zooplankton community became more diverse and no single taxon comprised more than 50% of the total biomass.

Seabirds and zooplankton

There was little correlation (r^2=0.335) between overall seabird abundance and zooplankton biomass as indicated by the weak positive trend shown in Figure 1.9.

Furthermore, abundances of individual seabird species groups were also weakly correlated to zooplankton biomass. Of 8,415 seabird sightings, 73% were flying, 25% sitting, and 2% feeding. Procellariiformes, puffins, alcids and storm-petrels had a weak positive correlation to zooplankton biomass, while northern fulmar, murres, black-legged kittiwakes, glaucous-winged gulls and larids had a weak negative correlation (Figure 1.10). The abundances of northern fulmars, glaucous-winged gulls, murres and black-legged kittiwakes were not associated with seasonal changes in zooplankton biomass (Figure 1.10). Conversely, the abundance of puffins, storm-petrels and dark shearwaters was highest during the months when zooplankton biomass was highest (Figures 1.8, 1.10). This is shown by elevated abundance of these species groups from May-August and suggests that seasonal environmental changes in this area make it a suitable habitat for these species. The relatively high seabird abundance in May (Figure 1.9: 30.893 birds km^{-2}; Figure 1.10: 20.100 birds km^{-2}), was due to one very large flock of storm-petrels May 2000. In addition, the relatively high northern fulmar abundance in April (Figure 1.10: 6.949 birds km^{-2}), was due to a large flock of this species in April 1998. The attempt to remove of these data points from the correlation analyses did not result in a great change in the r square value, such that it increased by < 0.1. Therefore these data points were retained in the correlation analyses.

Water column structure and seabirds

In winter and spring, mean temperature and salinity within the water column were ~5°C and 32.2, respectively (Figures 1.11a, 1.11b). During this period northern fulmars, murres and black-legged kittiwakes were the dominant species groups in the study area (Figures 1.5b, 1.6b, 1.7b). However, during summer and fall vertical stratification was strongest, owing to the presence of a pycnocline, which developed due to an increase in surface heating and freshwater discharge. The mean temperature above the pycnocline increased from ~5°C in the spring to 13°C in summer and the mean salinity above the pycnocline dropped from ~32.0 in May to 31.4 in August (Figures 1.11a, 1.11b). During this period puffins and storm petrels were the dominant species groups in the study area. In October the upper layer of the water column cooled to ~10°C. Little variation occurred in lower mixed layer temperature (1°C) and salinity (<0.050) throughout the year (Figures 1.11a, 1.11b).

Discussion

The observed seasonal changes in seabird abundance and species composition in relation to zooplankton biomass and physical properties of the water column in this study result from data collected over six years from October 1997 to October 2003 and are therefore a robust measure of the seasonal seabird species composition and mean abundance in the northern GOA. The data on zooplankton species composition and biomass may serve as an indicator of resource availability, which helps us understand

seabird habitat use. Furthermore, the measurements of seasonal changes in temperature, salinity and density depict the evolution of the physical properties of the water column leading to optimal conditions for the onset of the spring phytoplankton bloom. Therefore, this study presents a characterization of seabird habitat in the context of seasonal changes in seabird species composition and abundance.

The index of relative abundance of seabirds in this study is conservative because the survey area has been accounted for in each cruise to avoid biasing the data by region or season. Although a number of studies have previously documented seabird distribution in the GOA (Gould et al. 1982; Burger et al. 2004; Day and Prichard 2004; Hunt et al. 2005; Yen et al. 2005), count and analysis methodologies were not always clearly outlined, which can complicate interpretation of direct comparisons. Thus, the data comparisons presented here provide a more robust characterization of the overall trend in seabird distribution and habitat use in the northern GOA, and serve as a reference for the recent status of seabird community composition and abundance in this region during all seasons (winter, spring, summer, and fall).

The number of glaucous-winged gulls observed during the study period was low (0.03% of all seabird species observed); however, they composed 30% of the Laridae family and showed little seasonal variation in abundance during this study. Glaucous-winged gulls are omnivorous and are mainly distributed in near shore areas such as bays, estuaries and the intertidal zone (Hayward and Verbeek 2008); this may have contributed to their lower counts along the Seward line, which only covers a small portion of the

inshore habitat (Figure 1.2), and to their almost even distribution throughout the study period. Northern fulmars showed little variation in their abundance throughout the study period and may belong to a local population that overwinters in this region and settles at breeding colonies along the coast during spring and summer. Similar northern fulmar abundances along the Seward line in spring and summer may also be explained by the arrival of migrating and non breeding individuals that overwinter in other regions of the North Pacific (Hatch and Nettleship 1998; Hatch et al. 2010).

Murres and black-legged kittiwakes had higher abundance during the non-breeding season (October-April) than during the breeding season (May-August), and their abundance was uncorrelated with seasonal changes in zooplankton biomass. The higher abundance of murres and black-legged kittiwakes during the non-breeding period in the study area may be explained by overwintering birds that migrate from higher latitudes, in the Bering Sea and the Arctic Ocean, which are ice covered during winter (Hatch and Nettleship 1998; Ainley et al. 2002). Furthermore, murres and black-legged kittiwakes can disperse across the shelf during the non-breeding period because they are relieved from their colony duties. However, murres and black-legged kittiwakes must remain closer to their colonies during the breeding season because of their feeding behavior and energetic flight costs (Cairns et al. 1987; Ainley et al. 2003).

Results indicate that mean seasonal changes in overall seabird abundance in the northern GOA were not directly associated with seasonal changes in biological productivity, as indicated by zooplankton biomass. A combination of different factors

may explain this lack of association. The home range of seabirds is much larger than the area represented by the Seward line, and includes an along-shore component not represented in the surveys. Despite the systematic sampling of the seasonal cross-shelf seabird abundance and zooplankton biomass, the data coverage is limited to the width of the strip transect. In addition, the seasonal abundance of seabirds showed a high inter-annual and within season variation, unlike the zooplankton biomass which, despite the large inter-annual variation, showed a consistent pattern of decrease and increase in biomass by months (Figure 1.12a, 1.12c). If the data only included the year 2002, it may have been concluded that seasonal changes in seabird abundance were directly associated with the seasonal changes in productivity, since these changes were highly correlated (Figure 1.12b). On the other hand, if the data only included the year 2001, it would have been concluded that changes in seabird abundance were not associated with zooplankton biomass, because these changes were not correlated (Figure 1.12d). In addition, zooplankton production along the Seward line was higher in 2002 (25 g C m^{-2} y^{-1}) than in 2001 (19 g C m^{-2} y^{-1}) (Coyle, personal communication). The wide range of these results indicates the extreme temporal and spatial variability of the marine ecosystem in the northern GOA and highlights the difficulties in identifying linkages between seabirds and zooplankton biomass in the study area.

Another factor that may explain the lack of associations observed in this study is the relatively low biological productivity along the Seward line when compared to other areas in the GOA. Preliminary results from ecosystem models for the GOA (Coyle and

Hermann 2010) show that annual phytoplankton and copepod production along the Seward line are approximately one half of the estimates for areas farther west in the GOA (phytoplankton: about 100 g C m^{-2} y^{-1}, copepod: 15-20 g C m^{-2} y^{-1} along the Seward line; phytoplankton: 180-200 g C m^{-2} y^{-1}; copepod: about 25-30 g C m^{-2} y^{-1} in the western GOA). Therefore, the productivity along the Seward line may not be high enough to support large seabird abundances. Only 23% of the 8,415 seabird sightings during this study were sitting on the water and only 2% were actively feeding. This indicates that most birds in the study area may have been in transit to other areas in the GOA where resources might be more abundant and predictable.

Mean overall seabird abundance was relatively lower in the study area than in areas of the western GOA, around Kodiak Island and the Alaska Peninsula (Gould et al. 1982; Harrison 1982; Hunt et al. 2005). Around Kodiak Island seabird densities ranged from 35.4 birds km^{-2} in March to 148.0 birds km^{-2} in May (Harrison 1982), while seabird abundances in the study area ranged from 4.8 birds km^{-2} in October to 12.8 birds km^{-2} in May. In addition, greater seabird densities were also reported by Hunt et al. (2005) in the Kodiak Island vicinity, with seabird densities of 125 birds km^{-2} (May-August) and 128 birds km^{-2} (September-April). Along the Seward line, seabird abundance was 27.5 birds km^{-2} (May-August) and 22.5 birds km^{-2} (September-April), less than a quarter of the estimates reported by Hunt et al. (2005) in the Kodiak Island area. Gould et al. (1982) reported higher seabird densities along the Alaska Peninsula (spring: 145 birds km^{-2}; summer: 118 birds km^{-2}; fall: 138 birds km^{-2}) and around Kodiak Island (winter: 25 birds

km^{-2}; spring: 135 birds km^{-2}; summer: 72 birds km^{-2}; fall: 98 birds km^{-2}) than off the central Kenai peninsula coast (winter: 4 birds km^{-2}; spring: 6 birds km^{-2}; summer: 42 birds km^{-2}; fall: 5 birds km^{-2}). The higher seabird abundance in the western GOA, documented by these studies further suggests that biological productivity and seabird resource availability may be higher in the western GOA than in the Seward line vicinity. These data support the suggestions by Hunt et al. (2005) that the southwestern shelf around Kodiak Island is a richer foraging ground for seabirds than the shelf waters in the northeast GOA.

Dark shearwaters were not a dominant species in the study area and had a maximum abundance of 6.5 birds km^{-2} in May. In contrast, shearwaters were the dominant seabird species in all other studies conducted in the GOA (Gould et al. 1982; Harrison 1982; Burger et al. 2004; Hunt et al. 2005; O' Hara et al. 2006; Yen et al. 2005). Peak shearwater abundance along the Seward line was associated with maximum seasonal zooplankton biomass. However, these peak abundances only compare to the lowest abundance in the above previous studies (Gould et al.1982; Hunt et al. 2005). Furthermore, dark shearwaters do not breed from May-August, and are able to search a much larger area of the GOA because they are not restricted to central place foraging (Orians and Pearson 1979). Therefore, the fact that they are a dominant species in other regions of the GOA, but not in the area of this study, further indicates that while other regions of the shelf have high productivity, productivity in the Seward line vicinity is not high enough to support high abundances of dark shearwaters.

Several factors may contribute to the inconsistency in the seabird associations and zooplankton biomass throughout the seasons. In May and October changes in seabird abundance are influenced by migrating birds in and out of Alaska, respectively (Gould et al. 1982). In July and August changes in seabird abundance across the shelf are confounded by breeding birds, which are restricted to central place foraging due to increased energetic constraints (Stephens and Krebs 1986). In addition, more profitable potential seabird prey increases in abundance between May and October in the GOA. Mature capelin and herring, which can be within the seabird prey size, are abundant near shore, spawning at beaches from May through July, and larval sandlance and pollock become juveniles during this period (Wilson 2000; Brown 2002; Arimitsu et al. 2008). Furthermore, mature sandlance, which can be within the seabird prey size, and larger sizes of larval capelin and herring increase in abundance from August through November (Norcross et al. 2001; Doyle et al. 2002). An increase in Chaetognatha biomass in July and August and an increase in Cnidaria and Euphausiacea biomass in August and October indicate that predatory zooplankton may benefit from the shift in size from large (May-average length: 5 mm, average weight: 4 mg) to small (July-August-length range: 0.05-1.00 mm, weight range: 0.006 to 0.142 mg) copepods (Coyle personal communication) (Figure 1.8). Therefore, the association between zooplankton biomass and seabird abundance seems to be decoupled by an increase in abundance of forage fish, which feed on zooplankton during peaks in zooplankton biomass (May) and abundance (July and August) (Coyle and Pinchuk 2003; Armstrong et al. 2005; Wilson et al. 2006;

Doyle et al. 2009). This decoupling is influenced by an increase in food web complexity during the production season involving increases in diversity, biomass and life stages at multiple trophic levels in the GOA ecosystem.

The northern GOA marine ecosystem is very dynamic, with high temporal and spatial variability in the species composition of seabirds and zooplankton. This high variability results in large standard deviations and confidence intervals in the monthly means of seabird abundance and zooplankton biomass, respectively. Recurrent storms, eddies, strong currents and their interaction with the complex bathymetry in this region, result in periods of unpredictable mixing of the water column and patchy distribution of zooplankton and chlorophyll *a* (Okkonen et al. 2003; Childers et al. 2005; Coyle and Pinchuk 2005). Overall, the GOA shelf is a very productive marine ecosystem with millions of seabirds and one of the world's largest fisheries (Brodeur and Ware 1992, Springer et al. 1999). However, at a meso-scale (10-100's km) some areas of the GOA shelf are more productive than others (Coyle and Hermann 2010). The high degree of variability in this system and the overall levels of production in this study area do not favor high abundances of seabirds.

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Table 1.1. Month and year of GLOBEC-LTOP cruises in the northern GOA

Year	Month						
	March	**April**	**May**	**July**	**August**	**October**	**December**
1997						X	
1998	X	X	X	X†		X†	X*
1999	X	X	X		X†	X	X*
2000	X	X	X		X	X	X*
2001	X	X	X	X	X	X	
2002	X	X	X	X	X	X	
2003	X	X	X	X†	X	X	

* no zooplankton and physical data available

† no seabird data available

Table 1.2. Kruskal-Wallis and NDWD tests for differences in mean seabird abundance along the Seward line in the northern GOA, by month ($n = 33$) for the years 1997-2003; significant p-values are in bold ($p \leq 0.05$); the species categories used in the analyses are listed in the "major taxa" and "species group" columns below

Major taxa	Species Group	Chi-Square	Kruskal-Wallis	NDWD
All Species		8.164	0.229	0.146
Procellariiformes		12.699	**0.028**	**0.005**
	dark shearwaters	10.127	0.100	**0.021**
	storm-petrels	21.989	**0.000**	**0.003**
	northern fulmars	2.136	0.924	0.935
	black-footed albatross	15.960	**0.003**	**0.004**
	Laysan albatross	9.354	0.136	0.160
Alcidae		17.087	**0.002**	**0.000**
	murres	23.911	**0.000**	**0.001**
	puffins	24.539	**0.000**	**0.002**
	murrelets	11.63	**0.047**	0.053
Laridae		13.178	**0.022**	0.090
	black-legged kittiwakes	16.379	**0.003**	**0.002**
	glaucous-winged gulls	13.618	**0.014**	0.061
	terns	29.619	**0.000**	**0.001**

Table 1.3. Post-hoc non-parametric NDWD joint ranking multiple comparison test for differences in mean abundance of major seabird taxa along the Seward line in the northern GOA, by month for the years 1997-2003; significant p-values are in bold ($p \leq 0.05$)

Month	Species	March	April	May	July	August	October	December
March	All Species		1.000	0.246	0.949	0.997	1.000	0.9880
	Alcidae		0.999	1.000	0.999	0.914	**0.023**	1.000
	Procellariiformes		0.928	**0.005**	0.187	0.284	0.875	0.623
	Laridae		1.000	1.000	0.390	0.175	0.989	0.966
April	All Species			0.402	0.992	1.000	1.000	0.999
	Alcidae			1.000	1.000	0.989	0.091	0.996
	Procellariiformes			0.297	0.972	0.970	1.000	1.000
	Laridae			0.995	0.226	0.088	0.963	0.897
May	All Species				0.555	0.515	0.143	0.522
	Alcidae				0.993	0.812	**0.008**	1.000
	Procellariiformes				0.553	0.797	0.403	0.306
	Laridae				0.782	0.488	1.000	1.000

Table 1.3. Continued

Month	Species	March	April	May	July	August	October	December
July	All Species					1.000	0.861	1.000
	Alcidae					0.954	**0.004**	0.985
	Procellariiformes					1.000	0.991	0.996
	Laridae					0.986	0.949	0.909
August	All Species						0.983	1.000
	Alcidae						0.345	0.674
	Procellariiformes						0.989	0.994
	Laridae						0.740	0.591
October	All Species							0.953
	Alcidae							**0.0004**
	Procellariiformes							1.000
	Laridae							1.000

Table 1.4. Post-hoc non-parametric NDWD joint ranking multiple comparison test for differences in mean abundance of Procellariifomes along the Seward line in the northern GOA, by month for the years 1997-2003; significant p-values are in bold ($p \leq 0.05$)

Month	Species	March	April	May	July	August	October	December
March	shearwaters		0.433	**0.020**	0.790	0.850	0.877	0.611
	storm-petrels		0.996	**0.003**	**0.052**	**0.030**	0.403	0.981
	northern fulmars		1.000	1.000	1.000	1.000	1.000	0.944
	black-footed albatross		0.772	0.061	0.171	**0.004**	**0.011**	0.451
	Laysan albatross		1.000	0.728	1.000	1.000	0.996	0.507
April	shearwaters			0.957	0.954	0.984	0.994	0.998
	storm-petrels			0.060	0.447	0.285	0.837	1.000
	northern fulmars			1.000	1.000	1.000	1.000	0.988
	black-footed albatross			0.887	0.999	0.630	0.681	1.000
	Laysan albatross			0.878	1.000	0.998	1.000	0.746
May	shearwaters				0.221	0.465	0.643	0.584
	storm-petrels				0.763	0.987	0.837	**0.014**

Table 1.4. Continued

Month	Species	March	April	May	July	August	October	December
May	northern fulmars				0.996	1.000	1.000	0.933
	black-footed albatross				0.949	1.000	1.000	0.884
	Laysan albatross				0.740	0.417	0.972	1.000
July	shearwaters					1.000	1.000	0.999
	storm-petrels					0.996	1.000	0.239
	northern fulmars					1.000	1.000	0.994
	black-footed albatross					0.693	0.736	1.000
	Laysan albatross					0.982	1.000	0.447
August	shearwaters						1.000	1.000
	storm-petrels						0.994	0.133
	northern fulmars						1.000	0.973
	black-footed albatross						1.000	0.567
	Laysan albatross						0.968	0.159

Table 1.4. Continued

Month	Species	March	April	May	July	August	October	December
October	shearwaters							1.000
	storm-petrels							0.768
	northern fulmars							0.999
	black-footed albatross							0.626
	Laysan albatross							0.930

Table 1.5. Post-hoc non-parametric NDWD test for differences in mean abundance of Alcidae along the Seward line in the northern GOA, by month for the years 1997-2003; significant p-values are in bold ($p \leq 0.05$)

Month	Species	March	April	May	July	August	October	December
March	murres		1.000	0.522	0.268	0.088	**0.002**	0.999
	puffins		1.000	**0.010**	0.131	0.104	0.969	0.998
	murrelets		1.000	0.991	1.000	1.000	0.394	0.947
April	murres			0.633	0.389	0.147	**0.004**	1.000
	puffins			**0.002**	**0.035**	**0.033**	0.884	0.976
	murrelets			0.994	1.000	1.000	0.359	0.932
May	murres				1.000	0.998	0.680	0.623
	puffins				0.777	0.979	0.290	**0.012**
	murrelets				0.976	0.998	0.053	0.451
July	murres					0.978	0.288	0.328
	puffins					0.999	0.877	0.210

Table 1.5. Continued

Month	Species	March	April	May	July	August	October	December
July	murrelets					1.000	0.095	0.789
August	murres						0.903	0.094
	puffins						0.753	0.158
	murrelets						0.132	0.760
October	murres							**0.0007**
	puffins							0.998
	murrelets							0.864

Table 1.6. Post-hoc non-parametric test NDWD test for differences in mean abundance of Laridae along the Seward line in the northern GOA, by month for the years 1997-2003; significant p-values are in bold ($p \leq 0.05$)

Month	Species	March	April	May	July	August	October	December
March	black-legged kittiwakes		0.901	0.582	**0.018**	**0.002**	0.390	0.678
	glaucous-winged gulls		0.210	0.978	1.000	1.000	0.479	0.966
	terns		1.000	**0.001**	0.983	**0.013**	1.000	0.983
April	black-legged kittiwakes			0.998	0.780	0.362	0.988	1.000
	glaucous-winged gulls			0.807	0.059	0.088	1.000	0.596
	terns			**0.001**	0.983	**0.013**	1.000	0.983
May	black-legged kittiwakes				0.989	0.793	1.000	0.996
	glaucous-winged gulls				0.971	0.950	0.961	1.000
	terns				**0.001**	0.981	**0.001**	**0.001**
July	black-legged kittiwakes					0.963	0.999	0.474
	glaucous-winged gulls					1.000	0.269	0.946

Table 1.6. Continued

Month	Species	March	April	May	July	August	October	December
July	terns					**0.024**	0.983	1.000
August	black-legged kittiwakes						0.916	0.098
	glaucous-winged gulls						0.301	0.915
	terns						**0.013**	**0.024**
October	black-legged kittiwakes							0.972
	glaucous-winged gulls							0.883
	terns							0.983

Table 1.7. Post-hoc Tukey multiple comparison test of monthly mean zooplankton wet-weight biomass for major zooplankton taxa along the Seward line in the northern GOA 1997-2003; significant p-values are in bold ($p \leq 0.05$)

Month	Species	March	April	May	July	August	October
March	Total		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Crustacea		**0.000**	**0.000**	**0.000**	**0.000**	0.083
	Calanoida		**0.000**	**0.000**	**0.000**	**0.000**	0.747
	Euphausiacea		1.000	1.000	0.732	**0.008**	0.124
	Cnidaria		0.971	0.229	0.844	**0.000**	**0.000**
	Chaetognatha		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
April	Total			**0.000**	0.722	**0.000**	0.929
	Crustacea			**0.000**	1.000	0.883	**0.000**
	Calanoida			**0.000**	0.993	**0.001**	**0.000**
	Euphausiacea			1.000	0.805	**0.004**	0.072
	Cnidaria			0.690	1.000	**0.000**	**0.000**
	Chaetognatha			**0.000**	**0.000**	**0.000**	0.233

Table 1.7. Continued

Month	Species	March	April	May	July	August	October
May	Total				**0.000**	**0.000**	**0.000**
	Crustacea				**0.000**	**0.000**	**0.000**
	Calanoida				**0.000**	**0.000**	**0.000**
	Euphausiacea				0.660	**0.014**	0.184
	Cnidaria				0.9600	**0.014**	**0.000**
	Chaetognatha				0.260	0.693	**0.000**
July	Total					0.079	0.992
	Crustacea					1.000	**0.000**
	Calanoida					**0.000**	**0.000**
	Euphausiacea					**0.000**	**0.002**
	Cnidaria					**0.002**	**0.000**
	Chaetognatha					0.974	**0.000**

Table 1.7. Continued

Month	Species	March	April	May	July	August	October
August	Total						**0.003**
	Crustaceans						0.000
	Calanoida						**0.000**
	Euphausiids						0.857
	Cnidaria						1.000
	Chaetognatha						**0.000**

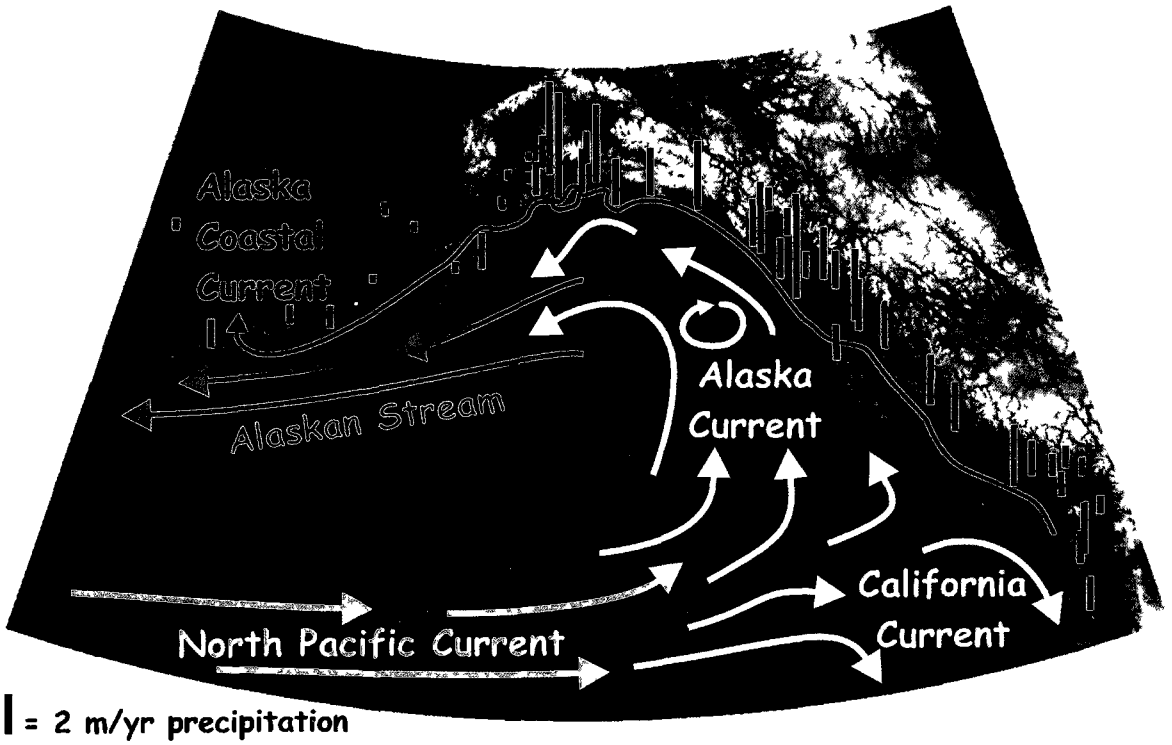


Figure 1.1. Circulation and coastal precipitation in the GOA (from Weingartner et al. 2005)

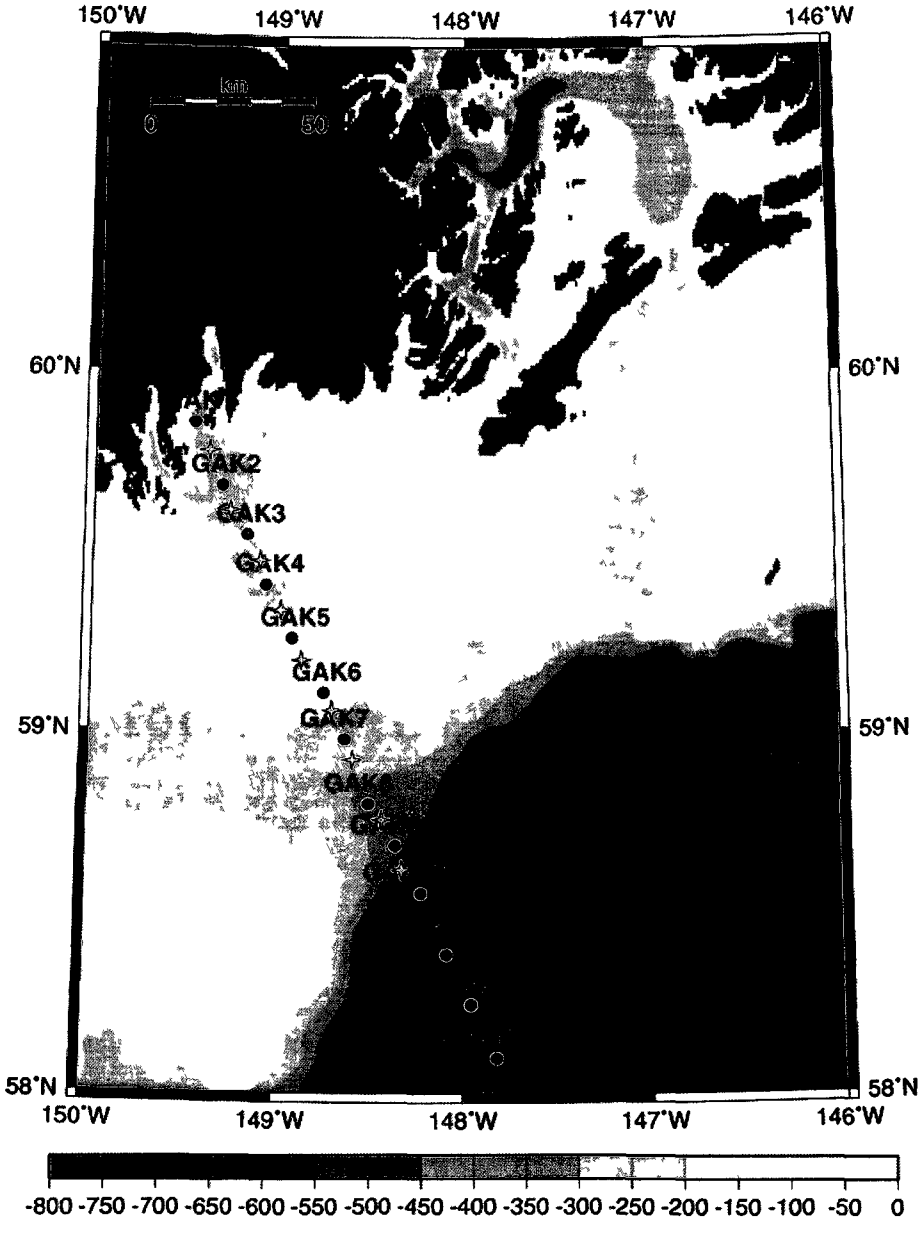
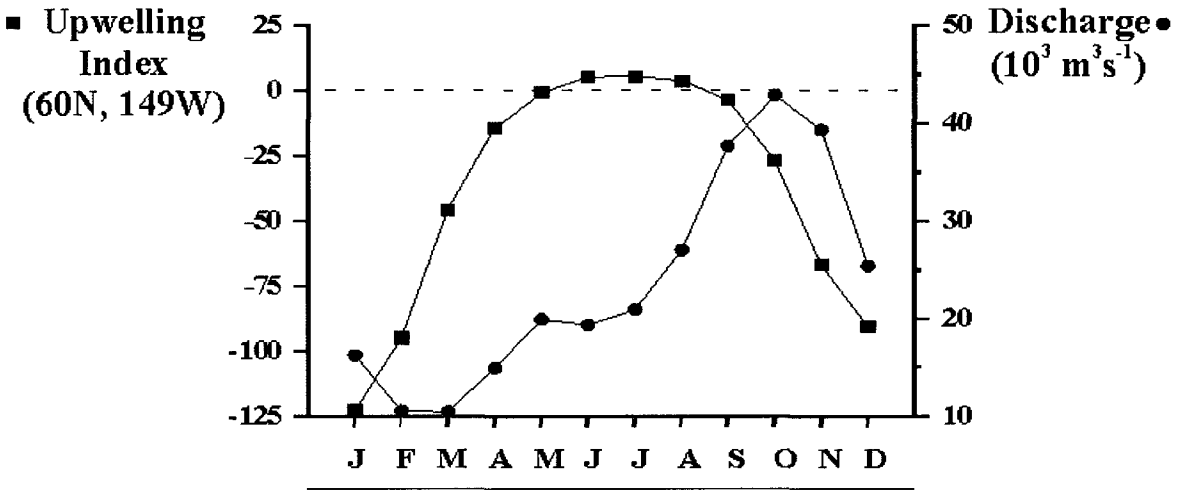


Figure 1.2. Transect along which seabirds were surveyed (Seward line-220 km). Black dots represent stations where zooplankton and hydrography data were collected. White stars represent stations where only hydrography data were collected. Scale bar indicates bottom depth (m).

a)



b)

March	April	May	July	August	October	December
Winter	Spring		Summer		Fall	Winter
Non-breed		Breed			Non-breed	

Figure 1.3. Annual upwelling index and freshwater discharge (10^3 m^3 s^{-1}) in the northern GOA (a) (from Weingartner et al. 2005); winter, spring summer and fall, seabird breeding and non-breeding seasons and their corresponding months (b)

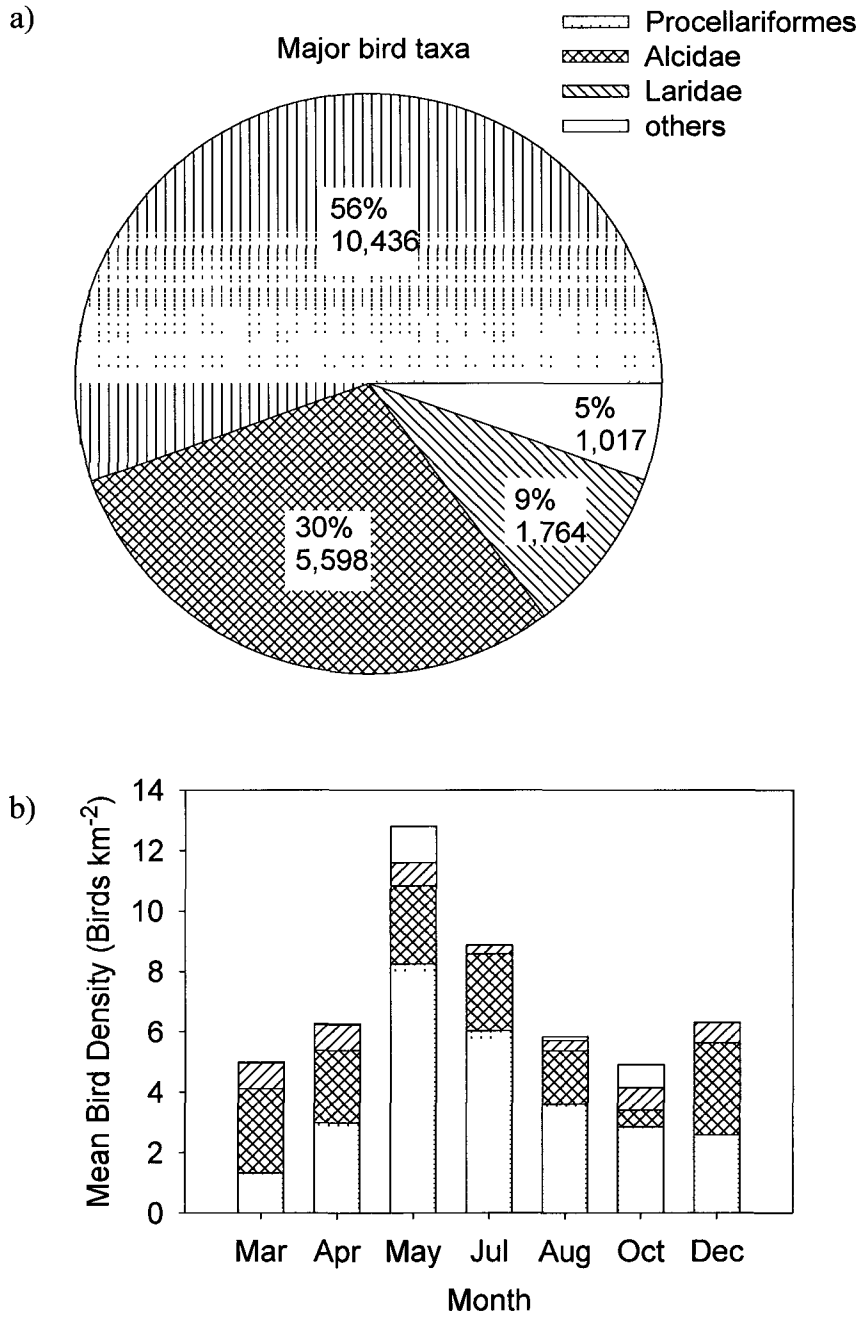


Figure 1.4. Percent composition and total number of birds counted (a), and monthly mean seabird abundance for the dominant taxonomic groups (b) along the Seward line in the northern GOA in 1997-2003

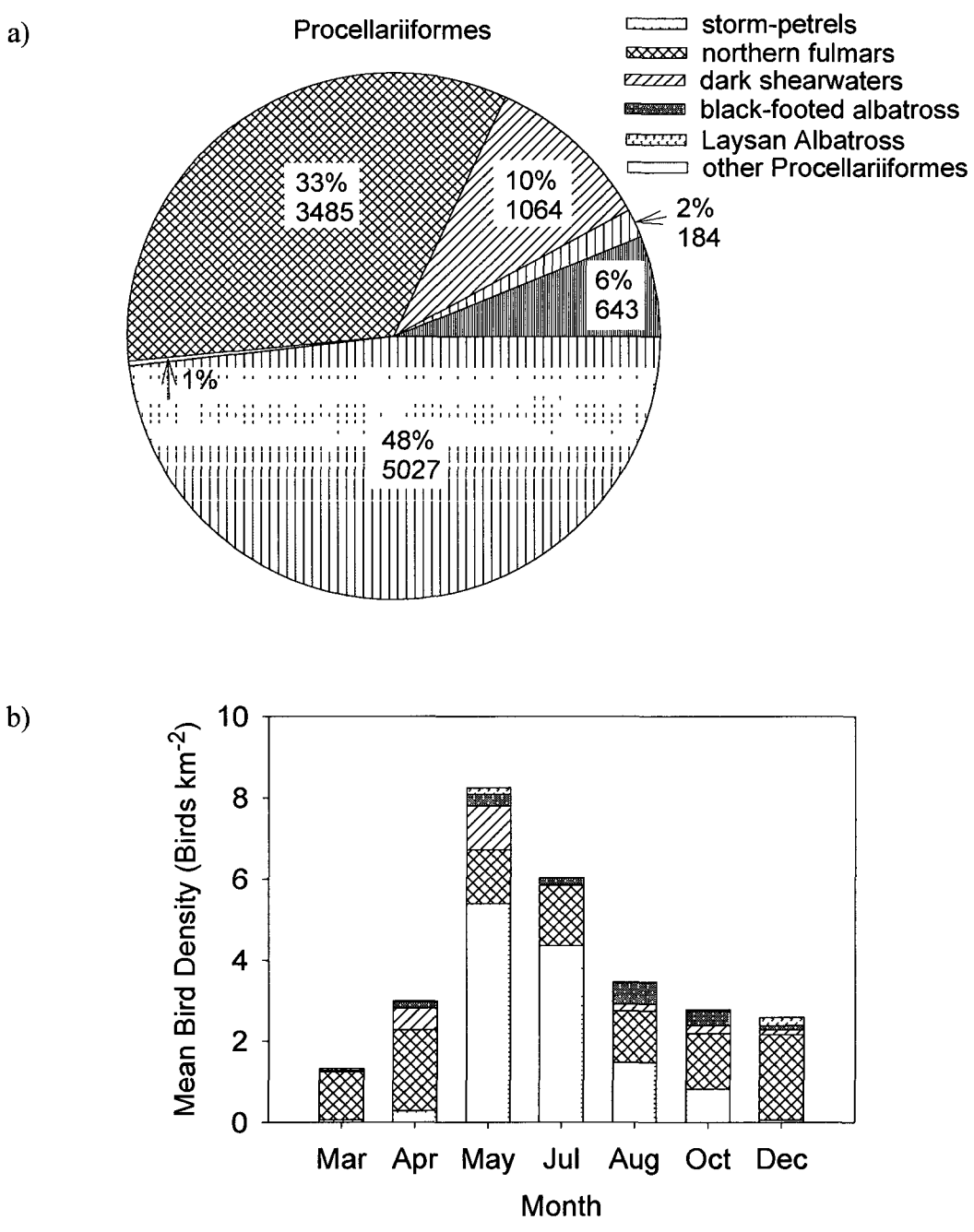


Figure 1.5. Percent composition and total number of birds counted (a) and monthly mean seabird abundance (b) of Procellariiformes along the Seward line in the northern GOA in 1997-2003

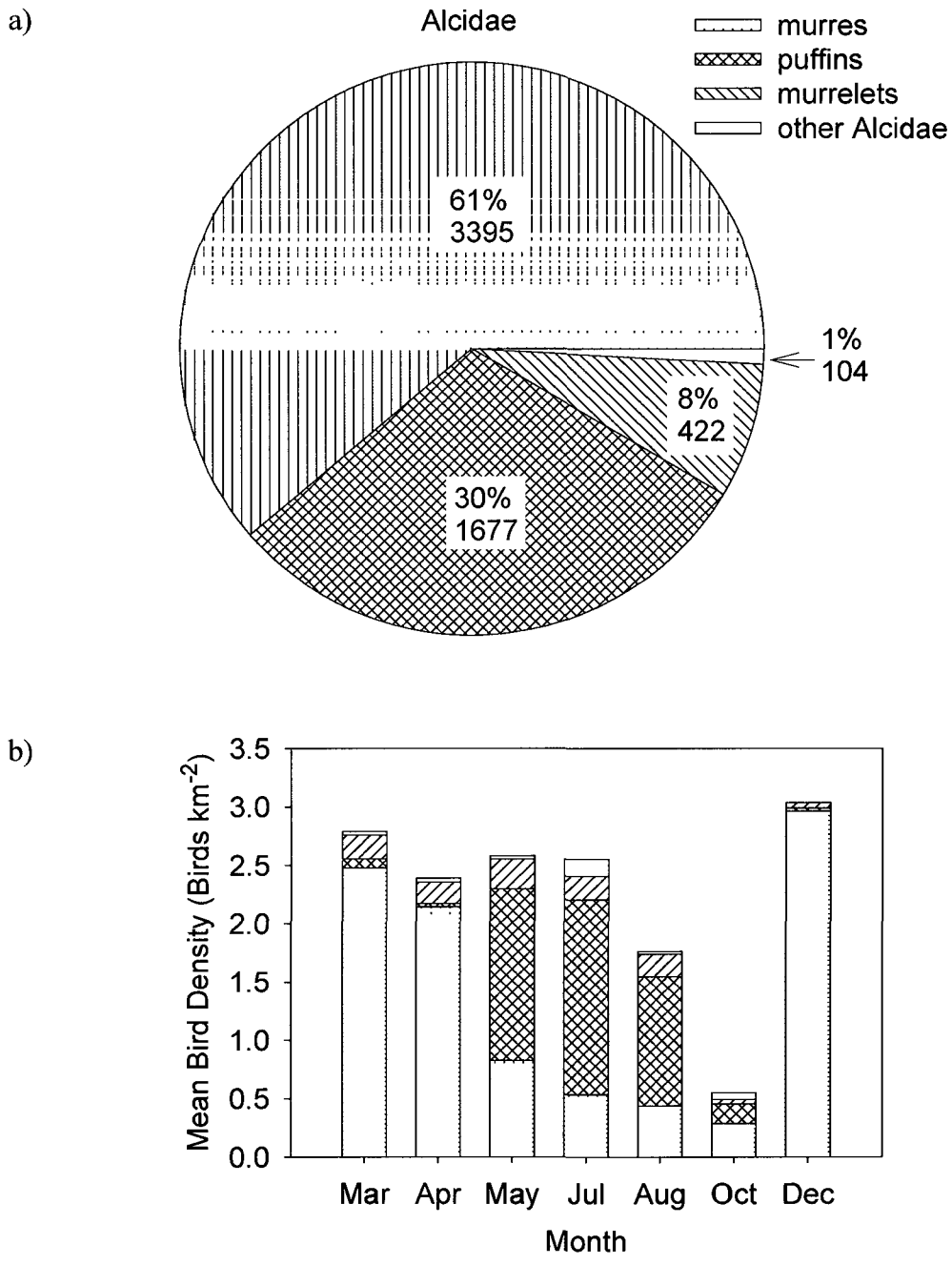


Figure 1.6. Percent composition and total number of birds (a), and monthly mean seabird abundance (b) of Alcidae along the Seward line in the northern GOA in 1997-2003

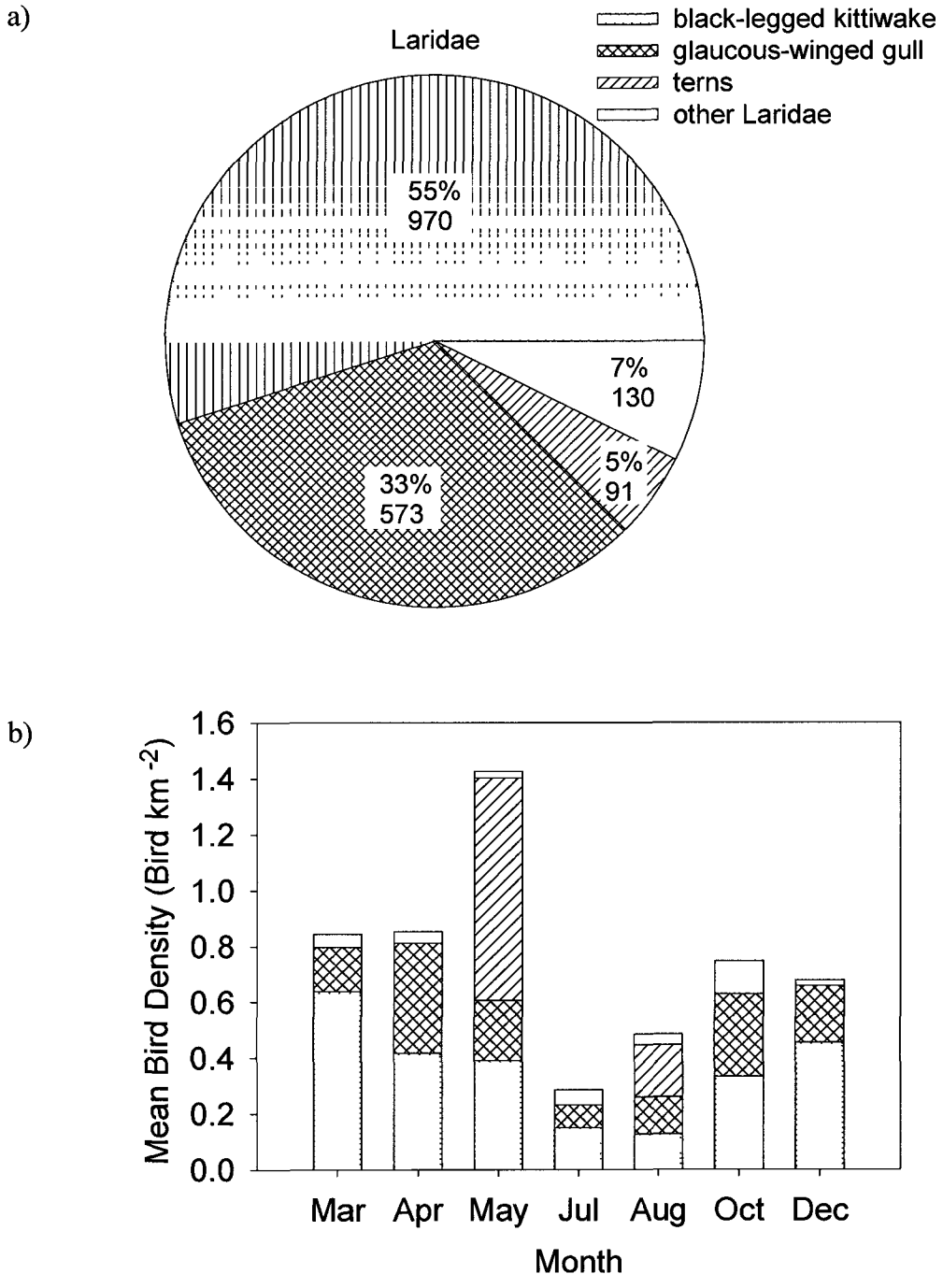


Figure 1.7. Percent composition (a), and monthly mean bird density (b) of Laridae along the Seward line in the northern GOA in 1997-2003

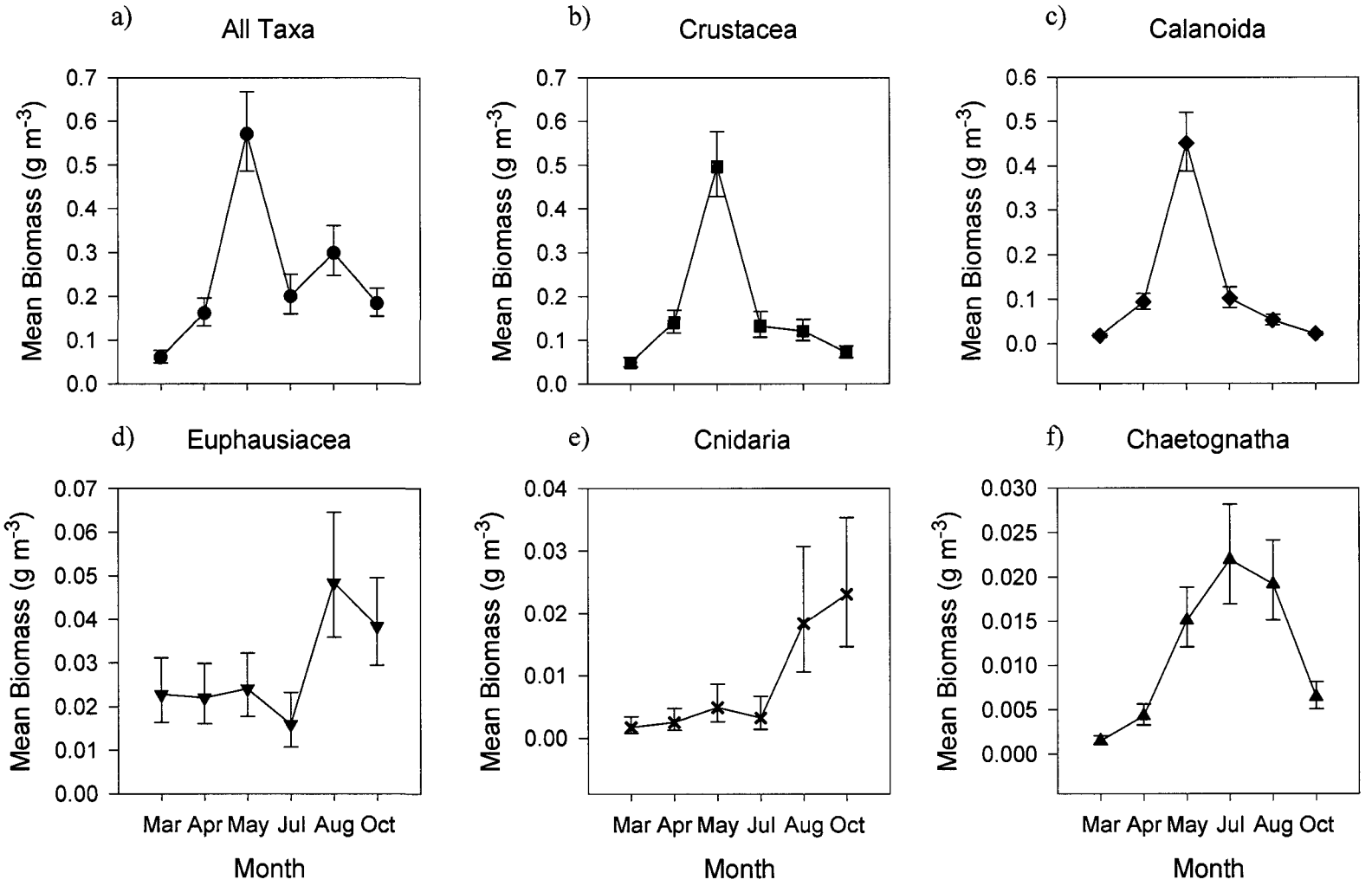


Figure 1.8. Monthly mean wet-weight biomass of major zooplankton taxa in the upper 45 m along the Seward line in the northern GOA (1997-2003), error bars indicate 95% confidence intervals

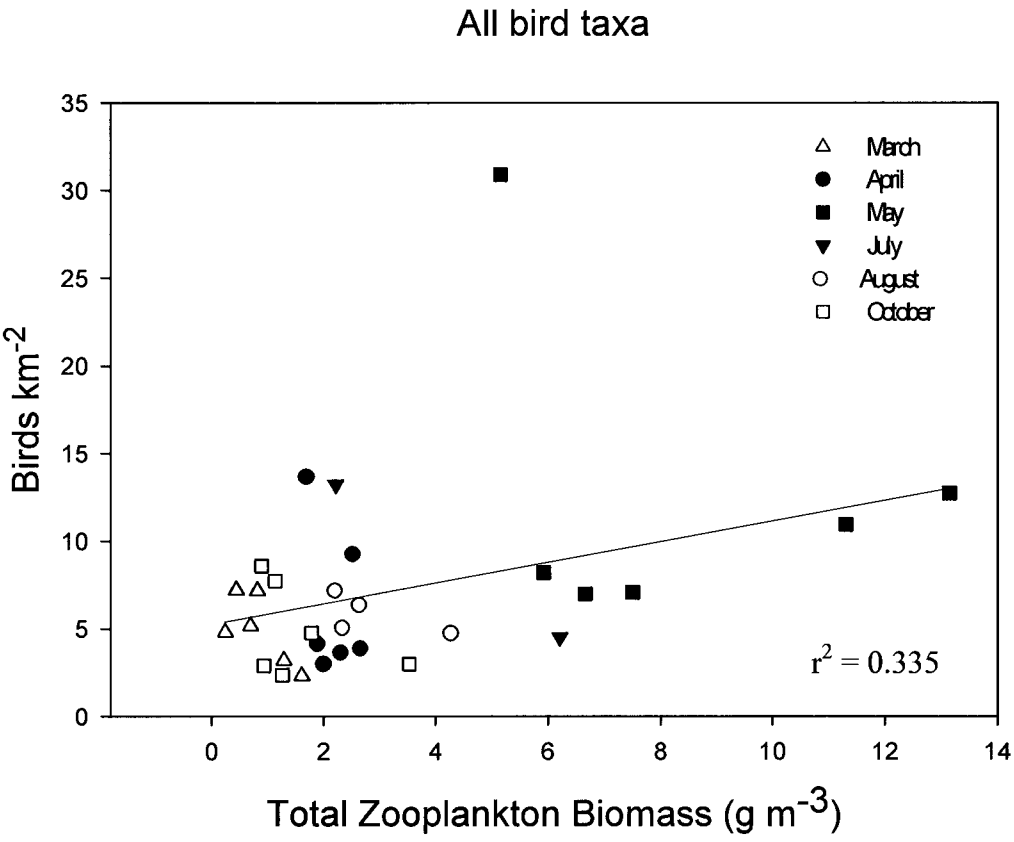


Figure 1.9. Correlation of total zooplankton biomass and bird abundance of all taxa for all cruises conducted along the Seward line in the northern GOA in 1997-2003. Cruises for which seabird abundance or zooplankton biomass data were not collected are not included in this plot (Table 1.1)

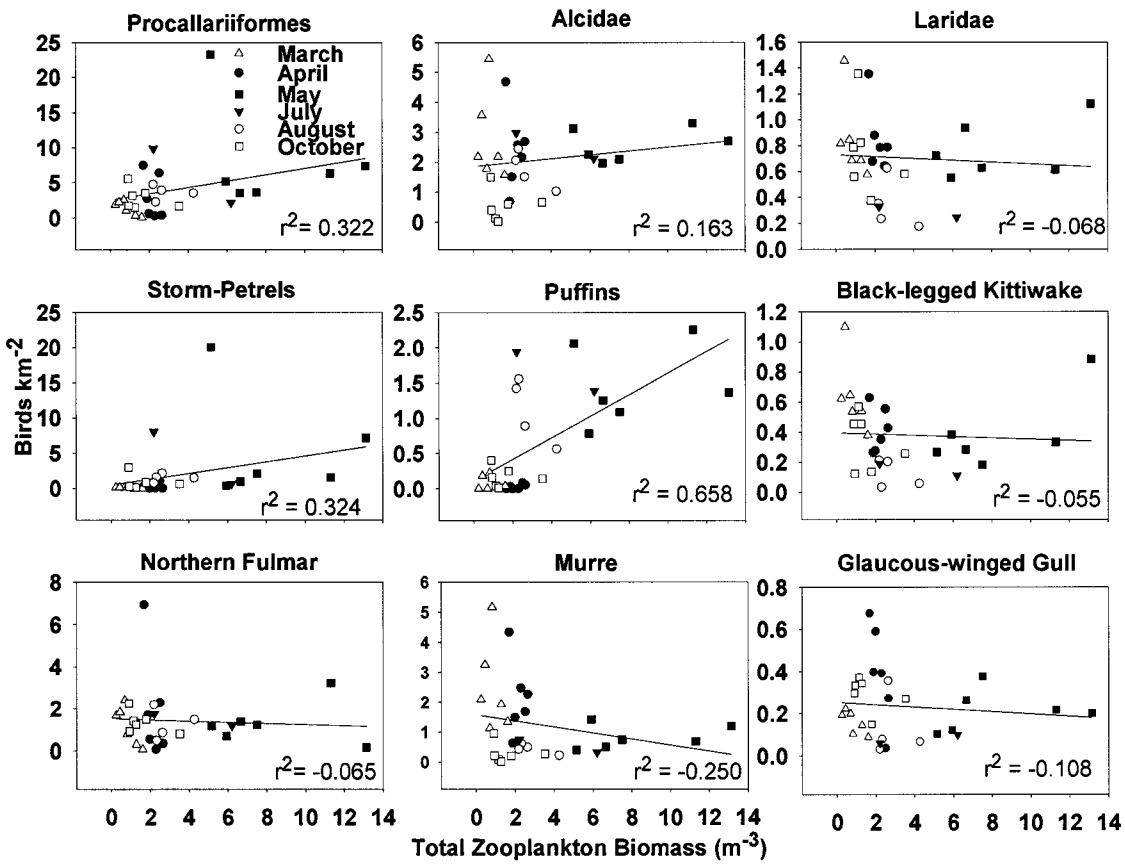


Figure 1.10. Correlation of total zooplankton biomass and bird abundance of species categories that comprise more than 80% of the major taxa (Procellariiformes, Alcidae, Laridae) for all cruises along the Seward line in the northern GOA in 1997-2003. Cruises for which seabird abundance or zooplankton biomass data were not collected are not included in this plot (Table 1.1)

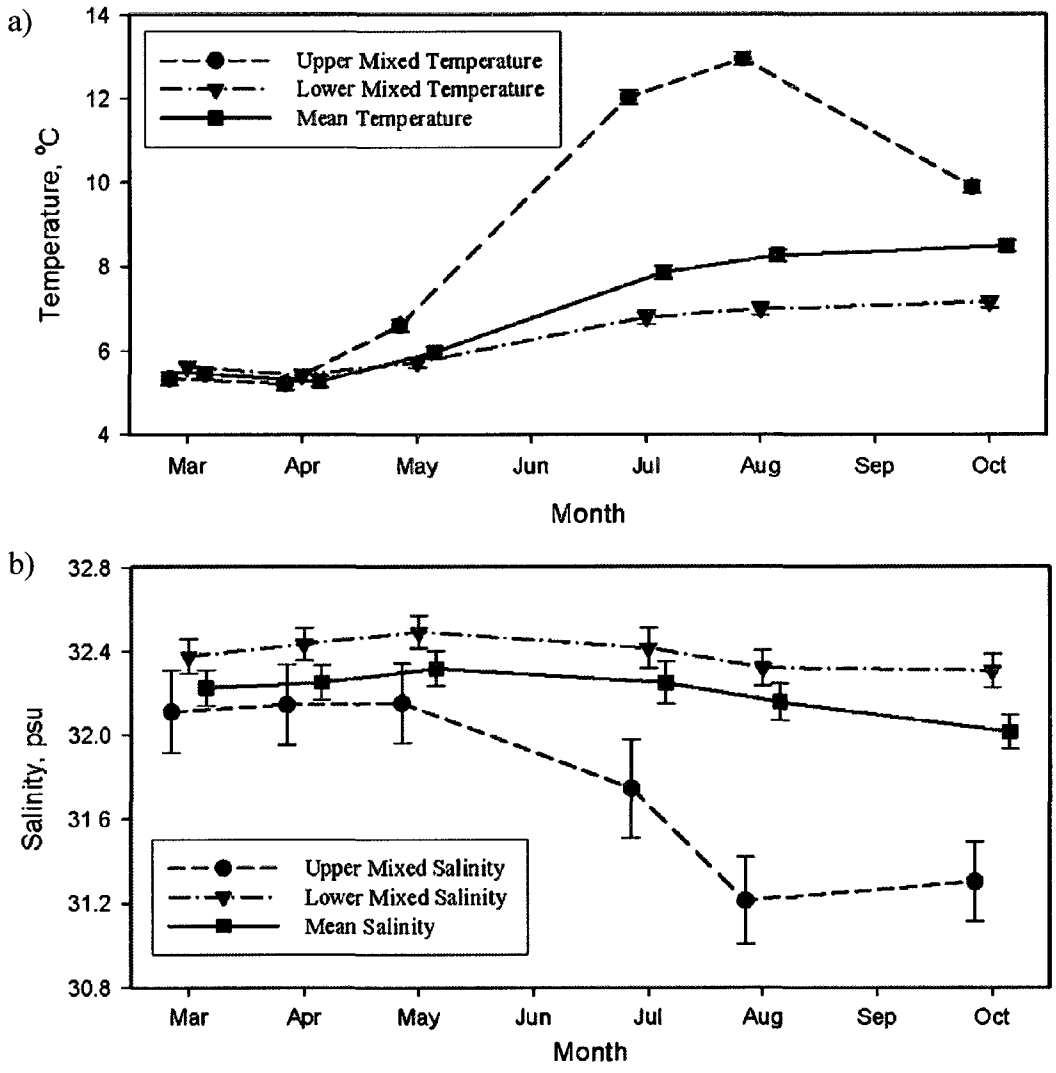


Figure 1.11 Seasonal changes in temperature (a) and salinity (b) above and below the pycnocline, and through the entire mixed layer (0-100 m), along the Seward line in the northern GOA in 1998-2003

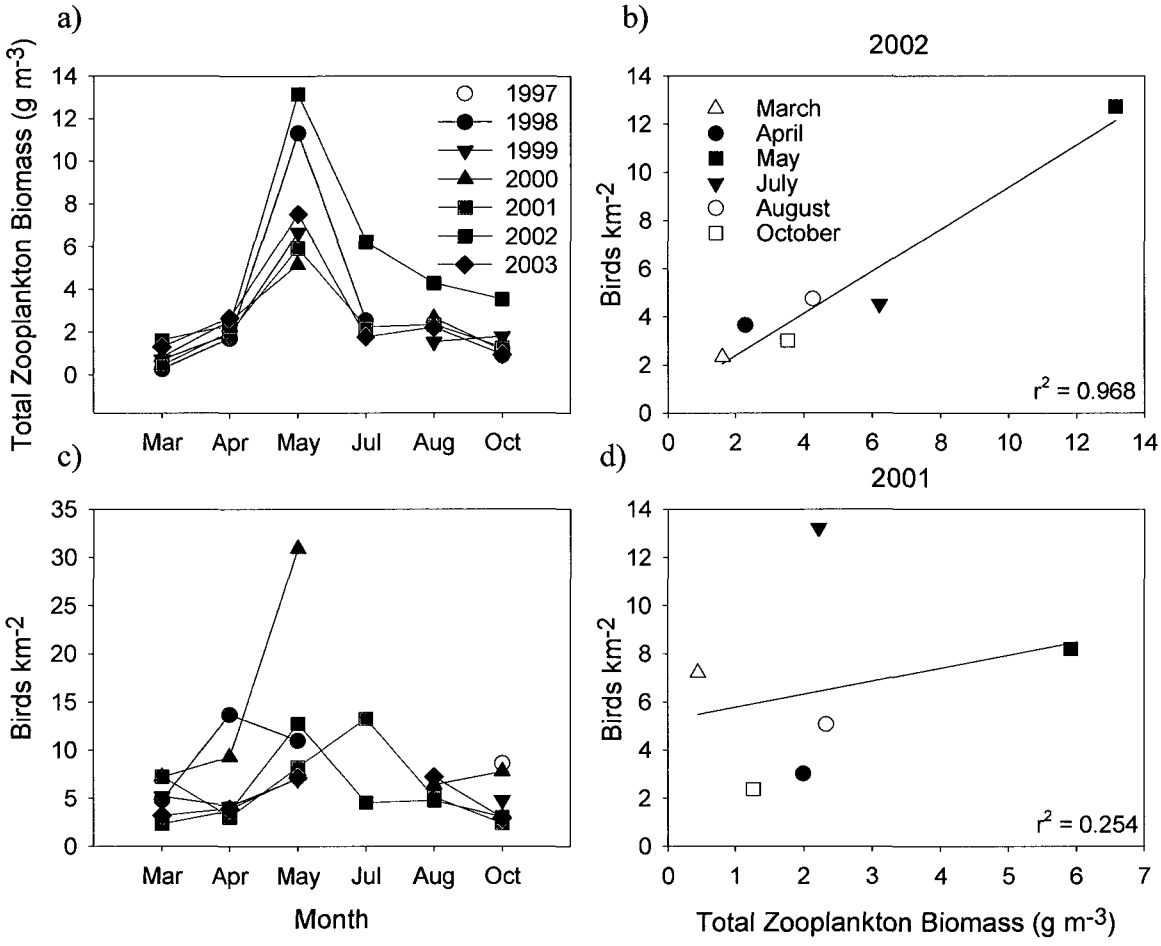


Figure 1.12. Total zooplankton biomass (a) and seabird abundance (c) by month from 1997-2003, and correlation between seabird abundance and total zooplankton for 2002 (b) and 2001 (d), along the Seward line in the northern GOA

CHAPTER 2. Habitat partitioning of seabird foraging guilds in the northern Gulf of Alaska in relation to water masses and zooplankton biomass[3]

Abstract

Data are presented on the cross-shelf distribution and abundance of seabird foraging guilds in northern Gulf of Alaska (GOA), and related to patterns in water mass properties and zooplankton species composition and biomass. At-sea surveys were undertaken to collect data on seabird abundance, zooplankton biomass and water mass properties (salinity and temperature) during winter (March) and early spring (April) from 2000 to 2003 in the northern GOA. Three zones (inner, middle and oceanic domain) were identified by mean salinity and overall zooplankton biomass, the latter of which increases from the inner shelf to the outer shelf. Highest density of divers, the most abundant seabird foraging guild throughout the study, occurred in the middle zone. Surface feeders were most abundant in the middle zone and oceanic domain, and surpassed the abundance of divers on only two surveys, when northern fulmars were the most abundant surface feeders. Murre abundance was positively correlated with the biomass of *Thysanoessa inermis*, and northern fulmars were associated with cephalopod paralarvae and the oceanic copepod *Eucalanus bungii*. Elevated biomass of *Thysanoessa*

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[3] Sousa L., Day R., Coyle K., Weingartner T., (2011) Habitat partitioning of seabird foraging guilds in the northern Gulf of Alaska in relation to water masses and zooplankton biomass. Prepared for submission in *Marine Biology*

inermis in March and April may be an important factor influencing habitat choice of wintering murres in the northern GOA.

Keywords: murres, northern fulmars, winter, squid, euphausiids, neritic, oceanic

Introduction

Seabird feeding methods can give insight into prey abundances and biological productivity in the marine environment (Ainley 1977; Wahl et al. 1989). For example, divers such as common murres are able to feed at depths greater than 100 m where euphausiids aggregate during daytime, while surface feeders such as the northern fulmars are only able to catch prey at the top few meters of the water column (Ashmole 1971; Hatch and Nettleship 1998; Ainley et al. 2002; Lu et al. 2003). Seabirds have adapted their feeding methods to an ever changing marine environment where productivity can be highly seasonal with extreme inter-annual and decadal variations (Mantua et al. 1997; Hyrenbach and Veit 2003). Within the marine environment, neritic and oceanic zones harbor distinct zooplankton, algae, fish communities, and water masses which can be used to characterize seabird habitat (Valiela 1995; Schreiber and Burger 2002). This study investigates the cross-shelf distribution and abundance of seabird foraging in guilds during winter and early spring, in relation to water mass properties and zooplankton biomass in the oceanic and neritic domains in the northern Gulf of Alaska (GOA).

The northern GOA is a very dynamic environment, and has a complex bathymetry with many canyons, troughs and a deep shelf (Weingartner et al. 2005). During fall and winter, intense westward alongshore winds cause onshore Ekman transport and coastal downwelling on the shelf. During spring and summer downwelling diminishes as winds relax (Stabeno et al. 2004; Weingartner et al. 2005). The main currents in this region are the Alaska Coastal Current (ACC) which flows westward within 20–50 km of the coast (Royer 1982; Weingartner et al. 2005), and the Alaska Current offshore Kodiak Island, which narrows and intensifies to become the Alaskan Stream, a western boundary current of the Subarctic Gyre (Reed 1984; Reed and Stabeno 1989).

The neritic zooplankton community in the northern GOA is characterized by high abundances of *Thysanoessa inermis*, *Metridia* spp., *Pseudocalanus* spp., and *Calanus marshallae*, while oceanic species are represented by *Euphausia pacifica*, *Eucalanus bungii*, *Neocalanus cristatus*, and cephalopod paralarvae (Coyle and Pinchuk 2005; Jorgensen 2007; Pinchuck et al. 2008). Nevertheless, cross-shelf transport of neritic and oceanic species can occur due to their exposure to different flow fields, to diel vertical migration and ontogenetic migration behaviors (Miller and Clemons 1988; Lu et al. 2003; Coyle and Pinchuk 2005; Pinchuck et al. 2008).

A wide variety of seabird foraging guilds inhabit the GOA. During the breeding season adults become aggregated near shore due to nest attendance, and during the non-breeding season they are able to disperse (Gould et al. 1982; Hunt et al. 2005; Day 2006). Resident species of seabirds remain in the northern GOA after the breeding season and

need to acclimate to a decrease in prey abundance. During this period resident species have to search for prey in an environment where contrast between high and low density prey patches is low and therefore more difficult to detect. Nevertheless, neritic and oceanic zones remain intrinsic components of the marine habitat. This study attempts to identify the physical and biological parameters that influence habitat choice of seabird foraging guilds when biological productivity is low and they are no longer restricted by breeding activities. Furthermore, this study identifies within season and inter-annual changes in seabird foraging guilds and their distribution and abundance in neritic and oceanic zones in relation to water mass properties and zooplankton biomass.

Methods

Study area

As part of the Global Ocean Ecosystems Dynamics (GLOBEC) Long Term Observation Program (LTOP) in the northern GOA, surveys were conducted along the Seward line (~220 km) during March and April from 2000-2003 (Figure 2.1, Table 2.1). These surveys were chosen because seabirds are not breeding during these months and therefore are not restricted by central place foraging (Poole 2005). This ensured that results would not be confounded by colony attendance and restricted foraging range associated with the seabird breeding season.

The study area can be divided into three zones: inner, middle shelves and oceanic domain (Figure 2.1). The inner shelf is highly influenced by freshwater runoff, and occasionally high salinity oceanic waters are advected into the middle shelf, which has a mixture of inner shelf and oceanic waters (Coyle and Pinchuk 2005). The oceanic domain has high salinity waters from the oceanic environment, and can be subject to the activity of mesoscale anticyclonic eddies that move along the shelf slope (Okkonen et al. 2003; Janout et al. 2009). The shelf in this area is broad (160 km wide) and deep, with bottom depths exceeding 150 m. Irregular bathymetry characterizes the shelf; water shoals from 250 m on the inner shelf to 150 m on the middle shelf before deepening again (Figure 2.1).

Seabirds

Seabirds were continuously counted during daylight hours (enough light for acceptable visibility), within a 300 m wide transect at a 90 ° angle from bow of the ship to its starboard side (Tasker et al. 1984). Birds were observed with the naked eye and with the aid of binoculars (10 x 42) from the bridge of the RV *Alpha Helix* (eye height = 7.7 m above sea surface), which cruised at ~18 km/h. At the beginning of each count interval, the ship's position, speed, Beaufort scale, and observational conditions were recorded (Appendix 1). A new count interval was initiated every five minutes following the previous count. Birds sighted within the survey strip were counted and identified to the lowest possible taxonomic level. Their positions and behaviors (sitting, feeding and

flying) were also recorded on a portable computer. Birds that approached the ship from behind were considered to be ship followers and were recorded only once and then ignored. Flying birds were counted using the "snapshot method" to prevent overestimation of seabird densities caused by the movement of flying birds through the transect (Tasker et al. 1984; Gould and Forsell 1989). The "snapshop method" consists of counting birds only once, by scanning the survey area at the beginning of each count interval (Tasker et al. 1984; Gould and Forsell 1989). Birds on the water were counted continuously because they are more difficult to detect with one scan. Flight direction of seabirds in relation to the course of the ship (Spear et al. 1992) was not accounted for during the surveys, and as a result there is not an estimate of absolute bird densities but rather an index of relative bird density. In this study, bird counts per km^{-2} are considered to be an index of relative abundance and are hereafter referred to as seabird abundance. The total of ocean surface scanned was 488 km^2 over 87 hours of effort.

Zooplankton

Zooplankton net samples were collected with a 1 m^2 Multiple Opening/ Closing Net and Environmental Sampling System (MOCNESS) (Wiebe et al. 1976) with 500 μm mesh nets. Zooplankton samples were taken at 13 stations spaced 18 km apart along the Seward line (Figure 2.1). The nets were fished at night and five oblique samples were collected in 20-m increments from 100 m depth to the surface. Samples were preserved in a 10% formalin seawater solution and stored for later analysis. All animals in the

samples were sorted and identified to the lowest taxonomic category possible, wet-weight biomass estimates were calculated following the methods of Coyle and Pinchuk (2005), and results were integrated for the upper 100 m of the water column. Furthermore, the short-term temporal (hours) and spatial (meters) mis-match between zooplankton sampling (night; diel vertical migration of some species) and seabird surveys (day) are unlikely to influence the analysis of this study because of the large temporal and spatial scales covered (6 months and 488 km^2).

Hydrography

Conductivity-temperature-depth (CTD) profiles were collected from surface to bottom at 1 m increments using a Seabird model 911 Plus fitted with conductivity, temperature and fluorescence sensors (Weingartner et al. 2005). Nineteen stations at ~8 km intervals were sampled along the shelf and slope; and 3 stations at ~18 km intervals were sampled in the oceanic domain (Figure 2.1). Mean temperature, salinity and sigma-t were calculated by averaging data from the upper 100 m. Pycnocline depths were determined by calculating the depth of greatest change in sigma-t through the water column. Upper and lower temperature, salinity and sigma-t were calculated by averaging the data from above and below the pycnocline.

Data analyses

Birds were assigned to one of two foraging guilds: 1) divers and pursuit plungers such as alcids, cormorants, and most shearwaters, which pursue prey underwater with their feet or wings for propulsion; 2) surface feeders including fulmars, gulls, albatrosses and storm-petrels, which capture prey at surface by dipping, surface seizing and pattering. Species that were rarely observed in transects and represented less than 0.05% of the seabird community were combined into their respective foraging guilds and are referred to as "other divers" or "other surface feeders". Surface plungers, such as pelicans and terns that enter the water using the momentum of a fall, were absent from the data. Kleptoparasitic birds represented less than 0.5% of the species and were not included in the analysis because they represent a small portion of the avifauna in the study region and because they show little association to environment variables (Ainley 1977; Wahl et al. 1989) (Table 2.2). Kleptoparasitic birds are birds that obtain their food by piracy, such as forcing birds to give up their pry or disgorge (Ashmole 1971).

Occasionally I was not able to distinguish between common murres (*Uria aalge*) and thick-billed murres (*Uria lomvia*), sooty shearwaters (*Puffinus griseus*) and short-tailed shearwaters (*Puffinus tenuirostris*), marbled murrelets (*Brachyramphus marmoratus*) and Kittlitz's murrelets (*Brachyramphus brevirostris*). Therefore, these species were combined observations into three categories: murres (*Uria* spp.), dark shearwaters (*Puffinus* spp.) and *Brachyramphus* spp..

The most frequent zooplankton groups that comprised the majority of the biomass in this study were included in the analyses. Cephalopoda paralarvae and Myctophidae (lantern fishes) did not satisfy these criteria. However, they were included in the analysis because they are important seabird forage species, and can be abundant in deep oceanic waters and serve as indicators of an oceanic environment (Ogi et al. 1980; Vermeer et al. 1987; Springer et al. 1996).

Only seabird sightings of the most frequent group sizes for each species (number of individuals per sighting) were included in the analyses. This helped reduce the variance in the seabird abundance data. Group size frequency for each species sighting was plotted and the probability of each group size to occur was calculated. Group sizes that comprised 95% of the sightings were included in the analyses and the ones that were less than 0.5% were excluded (Table 2.2).

The high heteroscedasticity, variability, overdispersion and zero-inflated data prevented the use of regression analysis, generalized additive models (GAMs) and generalized additive models for location scale and shape (GAMLSS) (Stasinopoulos and Rigby 2007) for the detection of linear or non-linear relationships between seabird abundance, zooplankton biomass and water mass properties. Logarithmic transformations and model adjustment using negative binomial distributions, or "quasi" link functions for zero-inflated and overdispersed data did not eliminate these problems (Venebles and Ripley 2002; Wood 2006). Therefore, non-parametric (for seabirds) and parametric (zooplankton and physical oceanography) analysis of variance and multiple

comparison methods were used to identify the differences between zones. Principal component analysis (PCA) was used to detect cruise groupings in relation to the abundance of surface feeders and divers, mean salinity, sigma-t and temperature in each zone. The mean salinity, sigma-t and temperature for each zone in each cruise were used in three separate PCAs. Separate PCAs were used because of unit differences in each of these measurements. The mean abundance of each bird species in each zone in each cruise (Table 2.1) was used in the PCA. PCA only included seabird species that occurred in all surveys so that any variance detected would be due to the species abundance in the three zones and not the presence/absence of species in each cruise. The calculated PCA scores for the bird and water mass data resulted in cruise groupings displayed in the PCA biplots. Seasonal variance in zooplankton biomass prevailed over spatial variability, so PCA was not used for zooplankton data. Canonical correlation analysis was used to determine the relationship between seabird abundance (response variable), water mass properties (explanatory variable) and zooplankton biomass.

The data collected in this study were used to characterize the spatial changes in seabird abundance and habitat. The alternative hypothesis that mean abundance of divers and surface feeders, mean zooplankton biomass and water mass properties are different among zones (inner shelf–IS; middle-shelf MS and oceanic domain-OD) was tested, in opposition to the null hypothesis that mean abundance of divers and surface feeders, mean zooplankton biomass and water mass properties are not different among zones.

These hypotheses were developed to identify the habitat choice of seabird foraging across the shelf and oceanic domain in the northern GOA.

Non-parametric Kruskal-Wallis analysis of variance (from here on referred to as Kruskal-Wallis test) was used to test the alternative hypothesis that the mean abundance of surface feeders and divers was different among zones (inner–IS (n=126), middle-MS (n=186) and oceanic domain–OS (n=117); n is the count of observation intervals in each zone) (Zar 1999). Furthermore, non-parametric Nemenyi-Damico-Wolfe-Dunn joint ranking multiple comparison test (from here on referred to as NDWD test) was used to identify which zones were significantly different (Hollander and Wolfe 1999; van de Wiel 2001), regarding the mean abundance of diver and surface feeders. Open-source statistical software R (R Development Core Team 2009) and the packages "coin" and "multcomp" (Hothorn et al. 2006; Hothorn et al. 2008) were used for Kruskal-Wallis test and NDWD, respectively. Tests were considered significant if $p < 0.05$. The p-value of the NDWD test for each pair-wise comparison is computed via Monte-Carlo resampling and accounts for the probability of a cumulative Type I error.

Analysis of variance was used to test the alternative hypothesis that overall mean zooplankton biomass, mean salinity, temperature and sigma-t were different among zones (IS (n=24), MS (n=30), OS (n=24), n is the total number of stations in each zone) (Zar 1999). Zooplankton analyses were performed using STATISTICA 6 software. Zooplankton biomass was power-transformed to stabilize the variance and tests were

considered significant if $p < 0.05$. Tukey's test was used to identify which months had significantly different mean zooplankton biomass.

Results

The inner, middle and oceanic zones presented differences in seabird abundance, mean salinity, sigma-t, temperature and zooplankton biomass (Table 2.3). Diver abundance was significantly different among the inner, middle and oceanic zones, with highest densities on the middle shelf. Surface feeder abundance was significantly lower on the inner shelf and higher on the middle and oceanic zones. Mean salinity and sigma-t were each significantly different among the three zones, and increased from the inner to the oceanic zone. Mean temperature was greatest in the middle shelf and lower in the inner shelf and oceanic zone. Mean salinity, sigma-t and temperature above and below the pycnocline produced the same trends as the mean for the upper 100 m. Therefore, means for below and above the pycnocline were not included in Table 2.3 and only the means for the upper 100 m were used the remaining stages of the analyses. The total zooplankton biomass in the middle zone was similar to the inner and oceanic zones, and the total zooplankton biomass in the oceanic zone was significantly higher than on the inner shelf.

The cross-shelf distribution patterns of divers and surface feeders reflected the abundances of murres and northern fulmars, respectively, which were the most abundant species in these foraging guilds (Table 2.4, Figures 2. 2, 2.6a-2.11a). The first and

second PC axes in the PCA of seabird species categories explained 93% of the variance among surveys and the most important variables on PC1 were the mean abundance of murres in the middle zone on the negative side, and northern fulmars in the middle and oceanic zones on positive side (Table 2.4). Thus, cruises with the highest abundance of murres on the middle zone appear on the negative side of the PC1 axis and cruises with the highest abundance of northern fulmars in the middle and oceanic zones appear on the positive side of that axis (Figure 2.2). The most important variables on PC2 were the mean abundance of murres and northern fulmars on the middle and oceanic zones on the negative side. Therefore, surveys that had the highest density of murres or northern fulmars on the middle and outer shelves appear on the negative side of the PC2 axis while cruises with lower numbers of murres and northern fulmars appear of the positive side of that axis.

The first and second PC axes in the PCA of temperature explained 99% of the variance among cruises; the most important variables on PC1 were mean temperature on the inner and middle zones on the positive side (Table 2.4). Therefore, cruises with the highest temperatures on the inner and middle zones appear on the positive side of the PC1 axis and the ones with low temperatures appear on the negative side (Figure 2.3a). The most important variables on PC2 were mean temperature in the middle zone on the positive side and on the oceanic zone on the negative side. Therefore, cruises with highest temperatures on the middle zone appear on the positive side of the PC2 axis and

cruises with low temperatures on the middle zone and high temperature on the oceanic zone appear on the negative side of the PC2 axis.

The first and second PC axes in the PCA analysis of salinity explained 92% of the variance among cruises; the most important variables on PC1 were mean salinity on the middle and oceanic zones on the negative side (Table 2.4). Therefore, cruises with the highest salinity on the middle and oceanic zones appear on the negative side of the PC1 axis and ones with low salinity appear on the positive side (Figure 2.3b). The most important variables on PC2 were mean salinity in the middle zone on the positive side and on the oceanic zone on the negative side. Therefore, cruises with highest salinity on the middle zone appear on the positive side of the PC2 axis and cruises with low salinity on the middle zone and high salinity on the oceanic zone appear on the negative side of the PC2 axis. PCA of sigma-t produced the same results as salinity and therefore are not shown.

Canonical correlation revealed significant relationships between the water mass properties, zooplankton biomass and the abundance of seabirds along the Seward line. Physical properties and zooplankton biomass explained 11.01% and 26.67% of the redundancy (the variance in seabird abundance explained by these data), respectively (Figures 2.4, 2.5). The influence of physical variables and zooplankton biomass on seabird species categories can be inferred from comparison of correlations between these variables and seabird abundance (Tables 2.5, 2.6). Murres were negatively correlated with sigma-t, while black-footed albatross and fork-tailed storm petrels were positively

correlated with sigma-t and temperature. Northern fulmars were positively correlated with salinity, temperature and sigma-t. Tufted puffins were positively correlated with salinity and sigma-t, and Laysan albatrosses were positively correlated with salinity. Murres were positively correlated with biomass of *Thysanoessa inermis* and shrimp, and negatively correlated with *Euphausia pacifica*, Myctophidae, Cephalopoda paralarvae, Chaetognatha, and overall zooplankton biomass (Table 2.6). Northern fulmars, dark shearwaters, fork-tailed storm petrels and black-footed albatross were positively correlated with Cephalopoda paralarvae and *Eucalanus bungii*.

The cross-shelf distribution of divers and surface feeders overlapped in March 2001 and April 2000 when surface feeder abundance was highest on the middle and oceanic zones (Figures 2.7a, 2.9a), and when high salinity oceanic water was advected onto the middle shelf and mean temperature in the upper 100 m was high (Figures 2.7b, 2.9b, 2.3a, 2.3b, Table 2.4). *Thysanoessa inermis* and Cephalopoda paralarvae were present in the middle shelf and their respective biomass was positively correlated with the abundance of murres and northern fulmars (Figures 2.7c, 2.9c, Table 2.6). The effect of the advection of saline water onto the shelf was also observed in the zooplankton species composition across the shelf. *Eucalanus bungii, Neocalanus cristatus*, and *Euphausia pacifica* had higher biomass seaward of the front, in the oceanic domain, than in the neritic domain landward of the front (Figures 2.7c, 2.9c).

Segregation of divers and surface feeders across the shelf occurred during all surveys other than March 2001 and April 2000, but under different physical

oceanographic settings. March and April 2002 had low salinity waters extending beyond the shelf break ($\geq$ 150 km) (Figures 2.8b, 2.10b), such that high salinity oceanic waters only occurred at depth and mean temperatures were low (Figure 2.3a, Table 2.4). Murres were the dominant species across the shelf while northern fulmar abundance was extremely low (Figures 2.8a, 2.10a). Biomass of oceanic zooplankton species was low (*Eucalanus bungii, Neocalanus cristatus, Euphausia pacifica*) and their distribution was restricted to the slope and oceanic zone, while neritic species *(Thysanoessa inermis)* were abundant across the shelf and aggregated in the middle shelf (Figures 2.8c, 2.10c). In March 2000 and April 2003 middle shelf temperatures were similar (Figure 2.3a, Table 2.4) and cross-shelf salinity gradients were higher (Figures 2.6b, 2.11b) than in March and April 2002 (Figures 2.8b, 2.10b). However, mean temperature in the upper 100 m was higher on the inner shelf in April 2003 than in March 2000 (Figure 2.3a, Table 2.4). Murres were abundant throughout the shelf and aggregated in the middle shelf, while northern fulmars only occurred in the oceanic domain (Figures 2.6a, 2.11a). *Eucalanus bungii* and *Euphausia pacifica* were restricted to the shelf-break and oceanic zone (Figures 2.6c, 2.11c). High salinity oceanic waters occurred at the surface beyond the shelf-break but not on the middle shelf (Figures 2.6b, 2.11b) as observed in March 2001 and April 2000 (Figures 2.7b, 2.9b).

Discussion

Physical environment

The magnitude and position of the salinity front across the shelf may be an important factor in making prey available to surface feeders. Similarities between salinity and sigma-t patterns across the shelf occur because cross-shelf density differences in the northern GOA in winter and early spring are mainly salinity driven and temperature variations are small (Weingartner et al. 2005). In March 2001 and April 2000 the salinity front was located at ~100 km from shore (Figures 2.7b, 2.9b) where the middle shelf is shallowest (Figure 1; GAK6 -150 m). Additionally, the slopes of the isohalines in the front in April 2000 were steepest throughout the water column (Figure 2.9b). In March 2000 and April 2003 the front was located at the shelf-break ~150 km from shore, where depths are greater than 650 m (Figures 2.6b, 2.11b). During these surveys, cross shelf advection of oceanic water may have interacted with the complex bathymetry of the shelf and made prey available at shallower depths for surface foragers (Figures 2.6a, 2.11a). On the other hand, prey appeared to be unavailable to surface feeders in March and April 2002, when there was no salinity front and only divers occurred in the low salinity – low temperature waters across the shelf (Figures 2.8a, 2.8b, 2.10a, 2.10b, 2.3a).

Mesoscale anticyclonic eddies can play an important role in the exchange of nutrients, organisms and iron between the shelf and GOA basin (Ladd et al. 2005;

Mackas and Coyle 2005; Janout et al. 2009; Wu et al. 2009). The interaction of eddies with the shelf break may result in changes in cross-slope flows and flow reversals, which may induce shelf water to flow along the trailing edge of the eddy (Janout et al. 2009); however, it is unclear if this cross-shelf exchange carries onto the continental shelf (Ladd et al. 2005). Mesoscale anticyclonic eddies were located at the shelf slope east of the Seward line in March 2002 and at the Seward line in April 2002. Low salinity and low temperature waters in the northern GOA are usually the result of coastal freshwater runoff (Royer et al. 2001; Weingartner et al. 2005). However, non-linear processes associated with eddy activity on the shelf break may have led to seaward flow of shelf water, contributing to the low salinity waters across the shelf in March and April 2002. Given the available data in this study, it could not be verified which mechanisms controlled the extent to which low salinity waters occurred across the shelf.

Prey (zooplankton distribution)

The onshore advection of oceanic water in April 2000 and March 2001 resulted in a distinct front in the middle zone where divers and surface feeders overlapped, indicating that food resources distributed in the middle shelf may have been available to both foraging guilds (Figures 2.7a, 2.9a). *Eucalanus bungii*, *Neocalanus cristatus*, and *Euphausia pacifica* are characteristic of oceanic waters while *Thysanoessa inermis* is characteristic of neritic waters (Coyle and Pinchuk 2005; Pinchuk et al. 2008), and cephalopod paralarvae are associated with high salinity waters from the oceanic domain

(r=0.481. p=0.0001, this study). *Thysanoessa inermis* and Cephalopoda overlapped in the middle shelf (Figures 2.7c, 2.9c) and are potential seabird prey that have been reported in the diet of murres in winter and northern fulmars, respectively (Prince and Morgan 1987; Elliot et al. 1990; Rowe et al. 2000). *Neocalanus cristatus* can be an important item in northern fulmar diet, and is selected over the less nutritious *Eucalanus bungii* (Jahncke et al. 2005). However, *Eucalanus bungii* was the only copepod positively correlated to northern fulmars in this study. These oceanic and neritic species partially overlapped in the middle shelf (Figures 2.7c, 2.9c). However, *Euphausia pacifica* overlapped to a lesser extent, because it spends most of the daytime below 100 m depth due to its diel vertical migration (Lu et al. 2003), and is therefore less likely to be advected onto to the shelf than *Eucalanus bungii* and *Neocalanus cristatus*, which are mainly distributed in the upper 40 m of the water column (Coyle and Pinchuk 2005).

Despite the low biomass of Cephalopoda caught in the MOCNESS, northern fulmars were positively associated with Cephalopoda, which consisted mostly of squid paralarvae. *Berryteuthis anonychus, Gonatopsis borealis, Gonatus onyx* and *B. magister* are reported to be the most abundant squid paralarvae in the GOA (Bower and Takagi 2004; Jorgensen 2007). *Berryteuthis anonychus* is a small gonatid squid (maximum mantle length=150 mm, Roper et al. 1984) and one of the most abundant squid in the GOA (Jorgensen 2007). They are a major prey item for fish, larger squid, birds and marine mammals (Ogi et al. 1980; Pearcy 1991; Kuramochi et al. 1993; Ohizumi et al. 2003), are most abundant in the upper 20 m of the water column, and show little evidence

of diel vertical migration (Bower and Takagi 2004). Furthermore, it is suggested that *Berryteuthis anonychus* migrates north as it matures in the northeast Pacific during spring (Bower et al. 2002). The abundance, size and behavior of this squid species suggest that they were a likely prey item contributing to the association between northern fulmars and cephalopod paralarvae.

Murres are generally classified as piscivorous (Bradstreet and Brown 1985; Byrd et al. 2005, Jahncke et al. 2008), but crustaceans can represent a large part of their diet during certain times of the year (Elliot et al. 1990; Ainley et al. 1996; Sydeman et al. 1997). Our results indicate that *Thysanoessa inermis* may be an important prey item for murres during winter and early spring in the northern GOA. *Thysanoessa inermis* are characteristic of the inner shelf habitat and are one of the dominant euphausiid species in the Gulf of Alaska (Coyle and Pinchuk 2005; Pinchuk et al. 2008). *Thysanoessa inermis* are mostly herbivorous and depend on the spring and summer phytoplankton bloom for accumulating lipids and achieving somatic growth (Falk-Petersen et al. 1981; Falk-Petersen et al. 2000). Furthermore, *Thysanoessa inermis* depend on their winter lipid reserves for reproduction in April and May (Pinchuk and Hopcroft 2006). The main forage fish species that comprise murre diet during late spring and summer in the GOA are: capelin (*Mallotus villosus*), Pacific sandlance (*Ammodytes hexapterus*), herring (*Clupea harengus*), and juvenile walleye pollock (*Theragra chalcogramma*) (Vermeer et al. 1987). During the winter and early spring forage fish biomass is lower in the GOA, due to different life history strategies of each species. Capelin over-winter in bays in

large inactive schools (January-March), and in April they begin their migration to the spawning grounds; however, their migratory routes are poorly known (Pahlke 1985; Brown 2002; Doyle et al. 2002). Adult sandlance are in a resting phase (in the sand) from February to May and pelagic sandlance larvae appear in late March and April (Haldorson et al. 1993; Robards et al. 1999). Herring spawn from May-June and over-winter in bays (Norcross et al. 2001). Adult pollock spawn from February to April, pelagic larvae appear in late April and May and transform into juveniles by the middle of summer. Therefore, forage fish are not very abundant across the shelf in winter and spring and murres may rely on lipid-rich *Thysanoessa inermis*, pa and adult females with attached spermatophores, as a profitable prey source.

Bird distributions

Given that murres were the dominant diver and northern fulmars the dominant surface feeder in this study, these species are used as representatives of each foraging guild throughout the discussion. The high abundance of murres and northern fulmars representing divers and surface feeders, respectively, agree with findings by Gould et al. (1982) and Day (2006), who also recorded high winter abundances of these species in the northern GOA. Black-legged kittiwakes and glaucous-winged gulls were frequent surface feeders along the Seward Line in this present study, but no associations were found between their abundance and potential prey, given little variation in their distribution and abundance across the shelf and throughout the surveys. Furthermore, it

is not clear why black-legged kittiwakes and glaucous-winged gulls remained in the study area when northern fulmars were nearly absent (March 2002, April 2002) (Figure 2.8a; 2.10a) given that all three are omnivorous and feed on offal and debris (Camphuysen and Garthe 1997; Hatch and Nettleship 1998; Hatch et al. 2009). However, northern fulmars have a highly developed olfactory sense while gulls do not (Hatch and Nettleship 1998). Therefore, fulmars and gulls may be responding to different environmental cues, despite their similarity as surface feeders and omnivores.

The dominance of murres and very low abundances of northern fulmars in March and April 2002 (Figure 2.8a, 2.10a), and the abundance of murres on the shelf and northern fulmars beyond the shelf-break in March 2000 and April 2003 (Figure 2.6a, 2.11a) show an association of these species to neritic and oceanic environments, respectively. These results agree with previous studies in the region, which found divers to be more abundant on the shelf than in the oceanic environment during the winter (Gould et al. 1982; Hunt et al. 2005). In the northeastern GOA O' Hara et al. (2006) found northern fulmars to be associated with coastal and oceanic environments (January-November) and with an affinity for high sea surface temperature and gradients. However, during May and June in the northeastern GOA, northern fulmars were only associated with the coastal environment (Yen et al. 2005). The difference among these results may be partly related to the seasons included in the analysis (breeding vs. non-breeding) and contrasting oceanographic processes in the northern (downwelling) and northeastern (upwelling) GOA (Stabeno et al. 2004; Weingartner et al. 2005).

Spatial and temporal mismatch between birds and zooplankton

Previous studies have observed prey aggregations as a result of current interaction with bottom topography. Coyle et al. (1992) found that tidal currents interacted with bottom topography aggregating euphausiids at ridges in the southeastern Bering Sea. Additionally, Hunt et al. (1998) found that tidal current interactions with bottom topography changed where different types of seabird prey were aggregated in Aleutian Island passes. Furthermore, the association of fronts and high abundances of seabirds has been extensively studied throughout the oceans (Schneider et al. 1987; Hunt 1991; Hunt et al. 1998; Ainley et al. 2005). However, the data in the present study do not show a spatial overlap among peaks in northern fulmar abundance, fronts and Cephalopoda, and occasional peaks in murre abundance, *Thysanoessa inermis* and low salinity. This lack of spatial overlap may be explained by the unpredictability of zooplankton aggregations and intensity of fronts, which are affected by physical forcing (Okkonen et al. 2003; Coyle and Pinchuk 2005; Weingartner et al. 2005). In the northern GOA intense storms can change the density gradient across the shelf in days, which means that fronts and high zooplankton density may occur in one area one day and be gone the next. In addition, large seasonal and inter-annual variability in wind stress and freshwater runoff can alter the onset of spring stratification and result in a mismatch between the phytoplankton and zooplankton bloom, which in turn affects zooplankton growth and recruitment for the following year (Liu and Hopcroft 2006; Pinchuk and Hopcroft 2007; Liu and Hopcroft 2008; Pinchuk et al. 2008). Therefore, the high variability in these physical and

biological conditions happening at multiple spatial and temporal scales in the northern GOA prevents the detection of consistent spatial overlap between seabirds and high zooplankton biomass along the Seward line.

Conclusions

Water mass properties and abundance of seabird foraging guilds were different across the shelf in the northern GOA. The high abundance of divers and surface feeders in conjunction with high total zooplankton biomass on the middle shelf suggests that this zone is an important habitat for both seabird foraging guilds. Murres were the most abundant seabird species during winter and early spring in the northern GOA and they were positively associated with *Thysanoessa inermis* biomass and low-density waters. Northern fulmars were the most abundant surface feeder in this region and were positively correlated with warmer saline waters and cephalopod paralarvae biomass. The middle shelf can be characterized as a transition zone between neritic and oceanic environments and supports high abundances of divers and surface feeders. Large ranges in salinity and temperature across the shelf occurred between cruises and influenced the distribution of neritic and oceanic zooplankton along the Seward line. The northern GOA is an important wintering area for murres, which may rely on *Thysanoessa inermis* during March and April, prior to the increase in forage fish abundance in this region. More information on the seasonal distribution and abundance of forage fishes and Cephalopoda

life stages are critical to improve the understanding of habitat use and prey selection by seabird foraging guilds in the northern GOA.

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Table 2.1. Month and year of GLOBEC-LTOP cruises in the northern GOA

Month	**Year**			
	2000	**2001**	**2002**	**2003**
March	HX228	HX239	HX254	
April	HX230		HX257	HX270

Table 2.2. List of species analyzed in this study and their corresponding foraging guilds, group size range, count and percent occurrence in order of descending percent occurrence; feeding methods described by Ashmole (1971) and Wahl et al. (1989); see methods section for the explanation on group size

Species Categories	Species	Feeding Strategy	Group Size	Bird Count	Percent (%)
murre	*Uria aalge, Uria Lomvia*	Diver	1-6	1389	41.24
northern fulmar	*Fulmarus glacialis*	Surface feeder	1-3	601	17.84
dark shearwater	*Puffinus griseus, Puffinus tenuirostris*	Diver	1-8	426	12.65
black-legged kittiwake	*Rissa tridactyla*	Surface feeder	1-3	310	9.20
fork-tailed storm petrel	*Oceanodroma furcata*	Surface feeder	1-6	188	5.58
Brachyramphus spp.	*Brachyramphus marmoratus, Brachyramphus brevirostris*	Diver	1-4	102	3.03
glaucous-winged gull	*Larus glaucescens*	Surface feeder	1-3	95	2.82
black-footed albatross	*Phoebastria negripes*	Surface feeder	1-2	81	2.41
other surface feeder	*Larus canus, Larus hyperboreus, Larus argentatus, Larus* spp., *Pterodroma inexpectata, Oceanodroma* spp.	Surface feeder	1-3	55	1.63

Table 2.2. Continued

Species Categories	Species	Feeding Strategy	Group Size	Bird Count	Percent (%)
tufted puffin	*Fratercula cirrhata*	Diver	1-3	50	1.49
Other diver	*Synthliboramphus antiquus, Cepphus columba, Ptychoramphus aleuticus, Aethia psittacula, Aethia cristatella, Aethia* spp., *Cerorhinca monocerata, Gavia pacifica, Phalacrocorax pelagicus, Phalacrocorax auritus, Phalacrocorax* spp.	Diver	1-4	45	1.34
Laysan albatross	*Phoebastria immutabilis*	Surface feeder	1-2	26	0.77

Table 2.3. Differences in mean diver and surface feeder abundance (birds km^{-2}), salinity, sigma-t, temperature (°C) and total zooplankton biomass (g m^{-3}) for all cruises by shelf zones (inner-IS, middle-MS and oceanic domain-OD) along the Seward line in March and April 2000-2003. Non-parametric Kruskal-Wallis and NDWD test were used for diver and surface feeders; ANOVA and Post-Hoc Tukey multiple comparison test were used for salinity sigma-t, temperature and total zooplankton biomass

Type	IS	MS	OD	Chi Square* and F**	p-value	Multiple Comparison
Divers	15.319	29.740	2.733	83.739	0.000	MS > IS > OS
Surface feeders	5.911	16.625	13.275	24.823	0.000	IS < MS ≈ OS
Salinity	31.866	32.426	32.678	69.168	0.000	IS < MS < OS
Sigma–t	25.183	25.590	25.846	81.889	0.000	IS < MS < OS
Temperature	5.049	5.396	4.894	21.071	0.000	MS > IS ≈ OS
Total zooplankton biomass	0.088	0.110	0.153	6.341	0.004	IS< OS, IS ≈ MS ≈ OS

* Chi square-Kruskal Wallis, ** ANOVA

Table 2.4. Results of principal componet analyses (PCA) including eigenvector (cumulative) proportions of variance explained by mean abundance of seabird species categories, mean temperature and mean salinity by zone: inner (IS), middle (MS) shelves and oceanic domain (OD). Only species with highest eigenvector loadings are shown.

	eigenvalue cumulative proportion		**eigenvector loadings**	
	PC1	**PC2**	**PC1**	**PC2**
Seabird species categories	0.71	0.93		
murres IS			0.14	-0.24
murres MS			-0.83	-0.53
murres OD			-0.02	-0.35
northern fulmar IS			0.07	-0.13
northern fulmar MS			0.41	-0.47
northern fulmar OD			0.33	-0.59
Temperature	0.95	0.99		
IS			0.87	-0.25
MS			0.47	0.64
OD			0.11	-0.73

Table 2.4. Continued

	eigenvalue cumulative proportion		eigenvector loadings	
	PC1	**PC2**	**PC1**	**PC2**
Salinity	0.73	0.92		
IS			0.21	0.15
MS			-0.34	0.94
OD			-0.92	-0.31

Table 2. 5. Correlation of physical variables with seabird abundance; values in bold are statistically significant

Seabird species categories	Mean Salinity	Mean Temperature	Mean Sigma-t
murre	-0.194	0.217	**-0.230**
northern fulmar	**0.503**	**0.278**	**0.459**
black-legged kittiwake	-0.012	0.218	-0.049
glaucous-winged gull	-0.063	-0.163	-0.153
Brachyramphus spp.	-0.132	0.138	-0.156
dark shearwater	0.208	0.128	0.188
fork-tailed storm petrel	0.359	**0.131**	**0.339**
black-footed albatross	0.373	**0.029**	**0.371**
Laysan albatross	**0.235**	0.181	0.205
other surface feeder	0.201	0.018	-0.206
tufted puffin	**0.244**	0.033	**0.241**
other diver	0.403	0.259	0.363

Table 2.6. Correlation of zooplankton biomass (g m^{-3}) with seabird abundance (birds km^{-2}); values in bold are statistically significant.

Seabird species categories	1	2	3	4	5	6	7	8	9	10	11	12	13
murres	**-0.253**	**0.406**	**-0.427**	0.024	-0.107	-0.189	-0.138	0.153	-0.185	**-0.316**	**0.409**	**-0.304**	**-0.429**
northern fulmar	-0.027	-0.010	0.029	-0.128	0.215	**0.329**	0.155	-0.189	0.222	-0.030	**-0.366**	**0.278**	-0.152
black-legged kittiwake	-0.172	0.084	-0.160	0.001	-0.074	-0.021	-0.083	0.019	-0.017	-0.126	-0.066	0.023	-0.190
glaucous-winged gull	-0.074	0.219	**-0.239**	-0.138	0.004	0.073	0.033	-0.024	-0.119	-0.100	**0.250**	-0.105	-0.080
Brachyramphus spp.	0.123	0.186	-0.209	-0.010	0.180	0.153	0.161	**0.226**	-0.126	-0.110	0.191	0.106	**-0.252**
dark shearwater	0.126	-0.040	-0.183	-0.064	**0.245**	**0.307**	**0.255**	-0.008	-0.014	0.057	-0.143	**0.236**	-0.137
fork-tailed storm petrel	0.141	-0.111	-0.113	-0.080	**0.268**	**0.431**	**0.316**	-0.063	0.086	0.085	**-0.226**	**0.317**	-0.085
black-footed albatross	0.176	-0.094	0.137	0.019	**0.259**	**0.337**	0.187	-0.146	0.194	0.040	-0.201	**0.230**	-0.056
Laysan albatross	**-0.238**	-0.010	0.034	0.067	-0.071	-0.076	-0.161	**-0.246**	0.106	**-0.233**	**-0.224**	-0.000	-0.121
other surface feeder	0.076	0.147	-0.072	0.137	-0.007	0.075	-0.011	0.141	-0.070	0.036	0.009	0.068	-0.108
tufted puffin	-0.116	-0.121	0.098	0.023	0.070	-0.025	-0.004	-0.083	0.188	-0.130	**-0.283**	0.184	0.187
other diver	-0.002	0.089	0.022	0.104	-0.121	-0.028	-0.063	0.042	-0.138	-0.011	-0.066	0.027	**-0.170**

1) Total zooplankton biomass, 2) *Thysanoessa inermis*, 3) *Euphausia pacifica* 4) *Thysanoessa spinifera* 5) *Neocalanus cristatus*, 6) *Eucalanus bungii*, 7) *Neocalanus plumchrus* and *Neocalanus flemingeri* 8) *Metridia* spp. 9) Cnidaria, 10) Chaetognatha, 11) Shrimp 12) Cephalopoda paralarvae, 13) Myctophidae

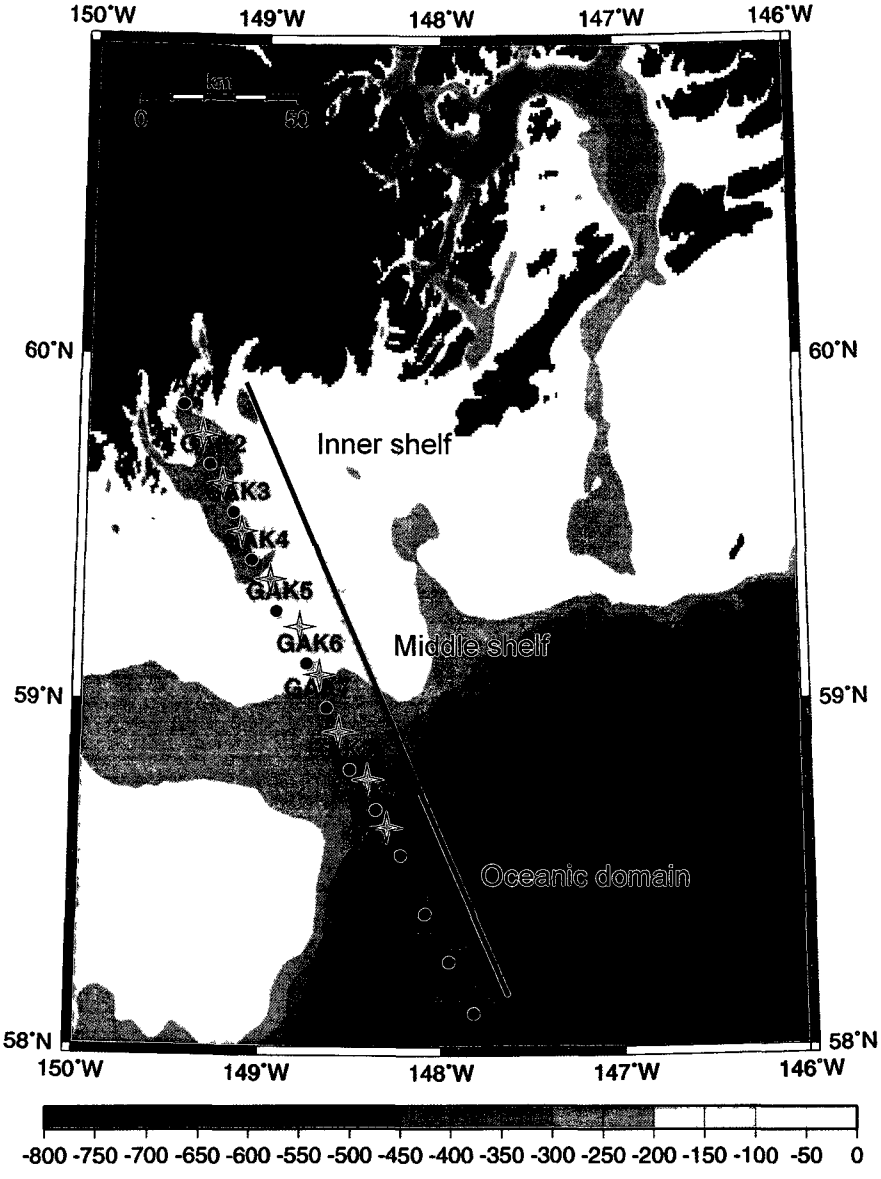

Figure 2.1. Transect where seabirds were surveyed along the Seward line (220 km). Black dots represent stations where zooplankton and physical oceanography data were collected. Stars represent stations where only physical oceanography data were collected. Colored lines indicate the three zones (black-inner, red-middle, blue-oceanic) and scaled colored bar indicates bottom depth. Scale bar indicates bottom depth (m).

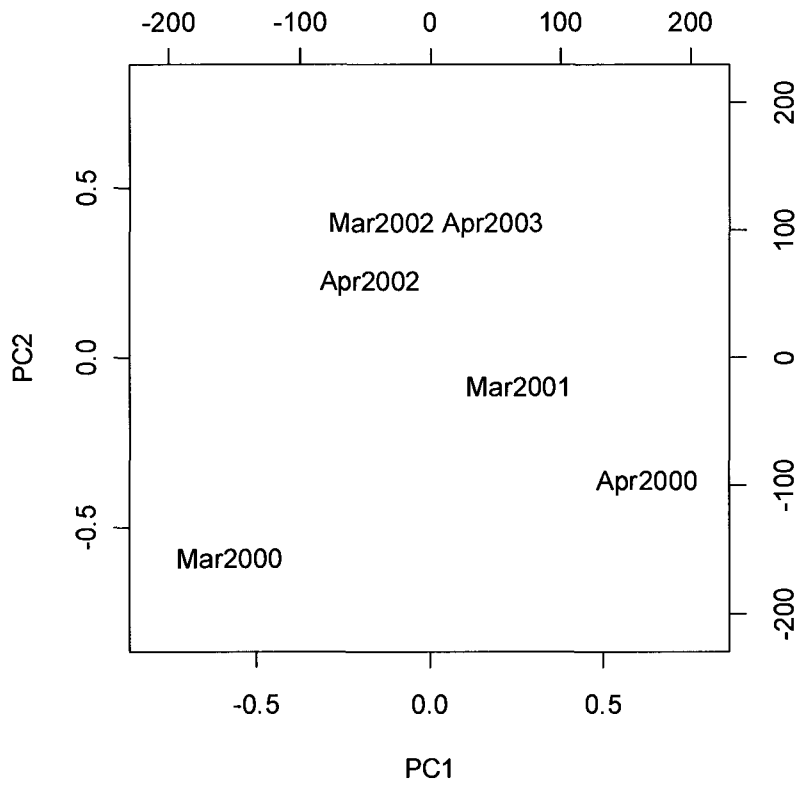

Figure 2.2 PCA biplot showing the differences among surveys (March 2000, 2001, 2002; April 2000, 2002, 2003) as explained by the variances in mean abundance of seabirds in the inner, middle and oceanic zones

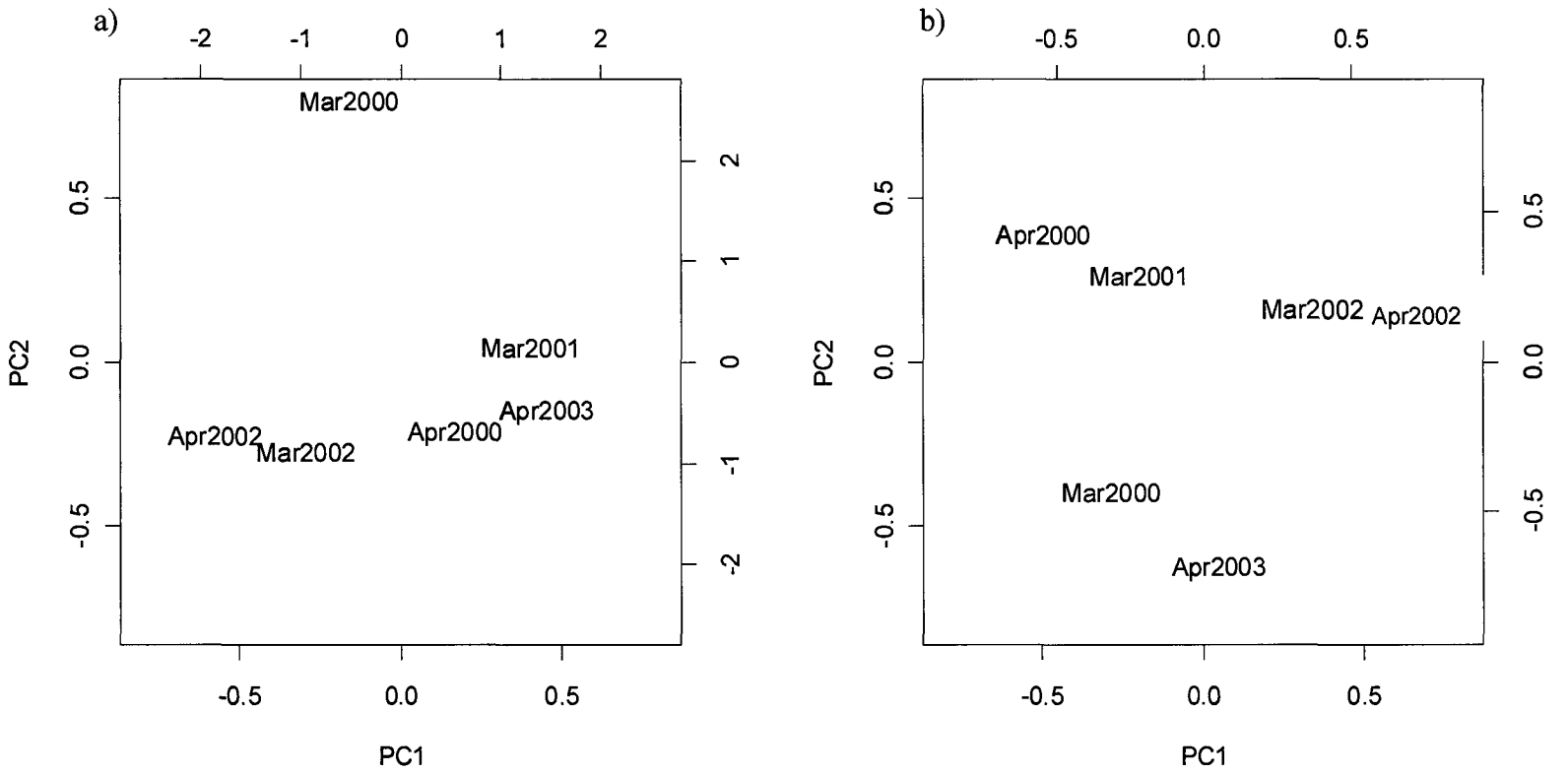

Figure 2.3 PCA biplots showing the differences among surveys (March 2000, 2001, 2002; April 2000, 2002, 2003) as explained by the variances in mean temperature (a) and salinity (b) in the inner, middle and oceanic zones

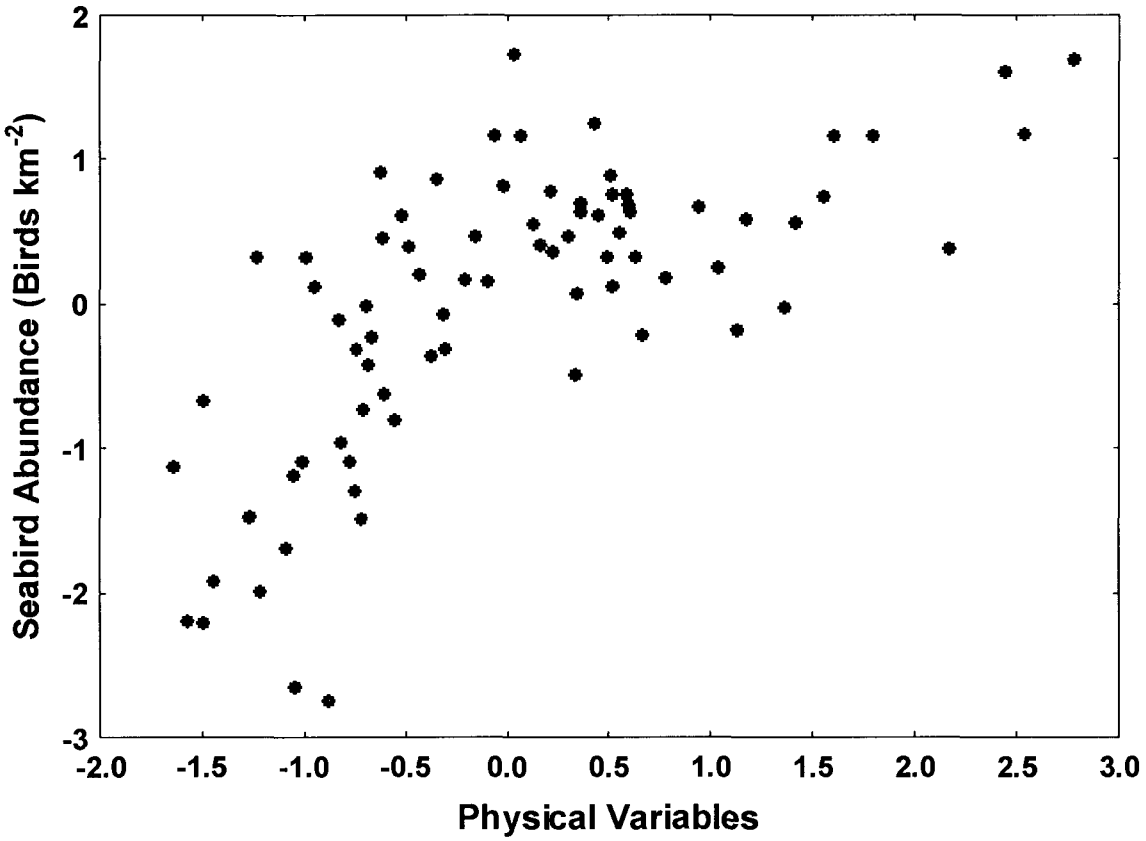

Figure 2.4 Physical and seabird abundance canonical variables along the Seward line in the northern GOA; number of cases (n) = 78, canonical R = 0.690, total redundancy = 11.01%, p-value = 0.003

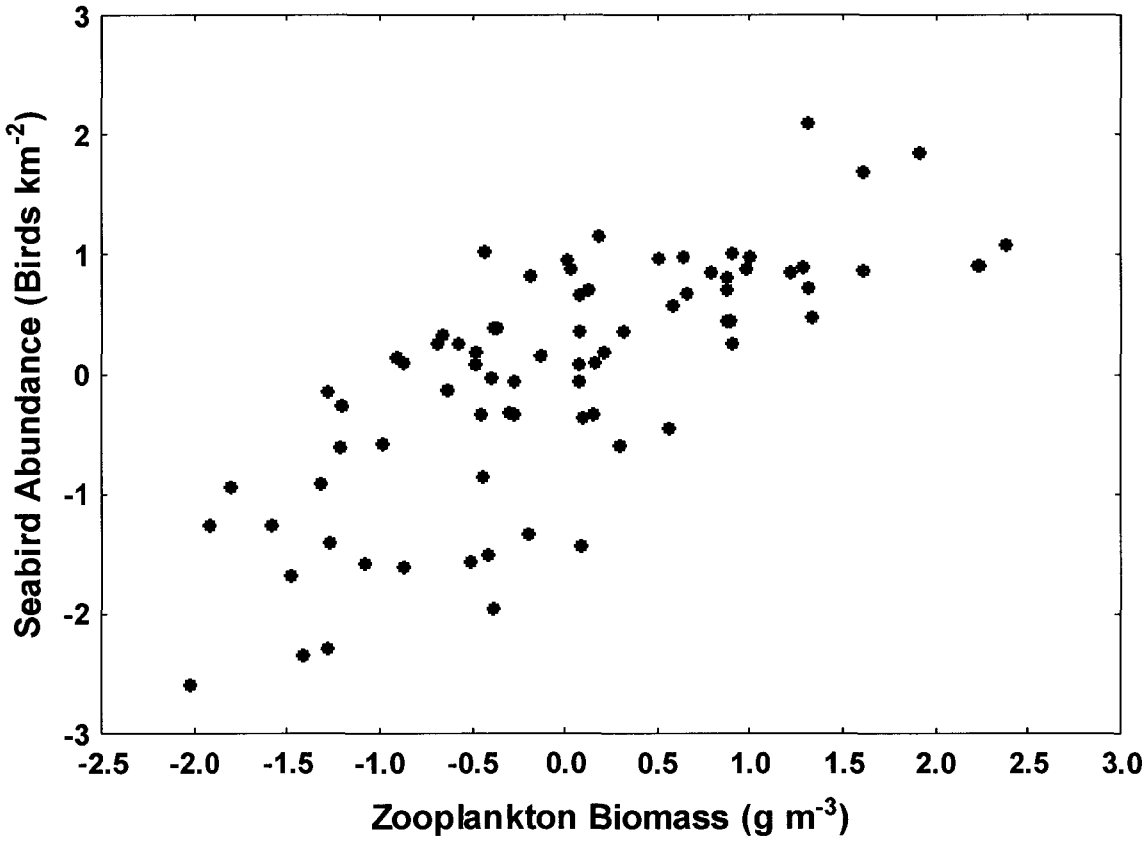

Figure 2.5. Zooplankton biomass and seabird abundance canonical variables along the Seward line in the northern GOA; number of cases (n) = 78, canonical R = 0.741, total redundancy = 26.67%, p-value = 0.0001

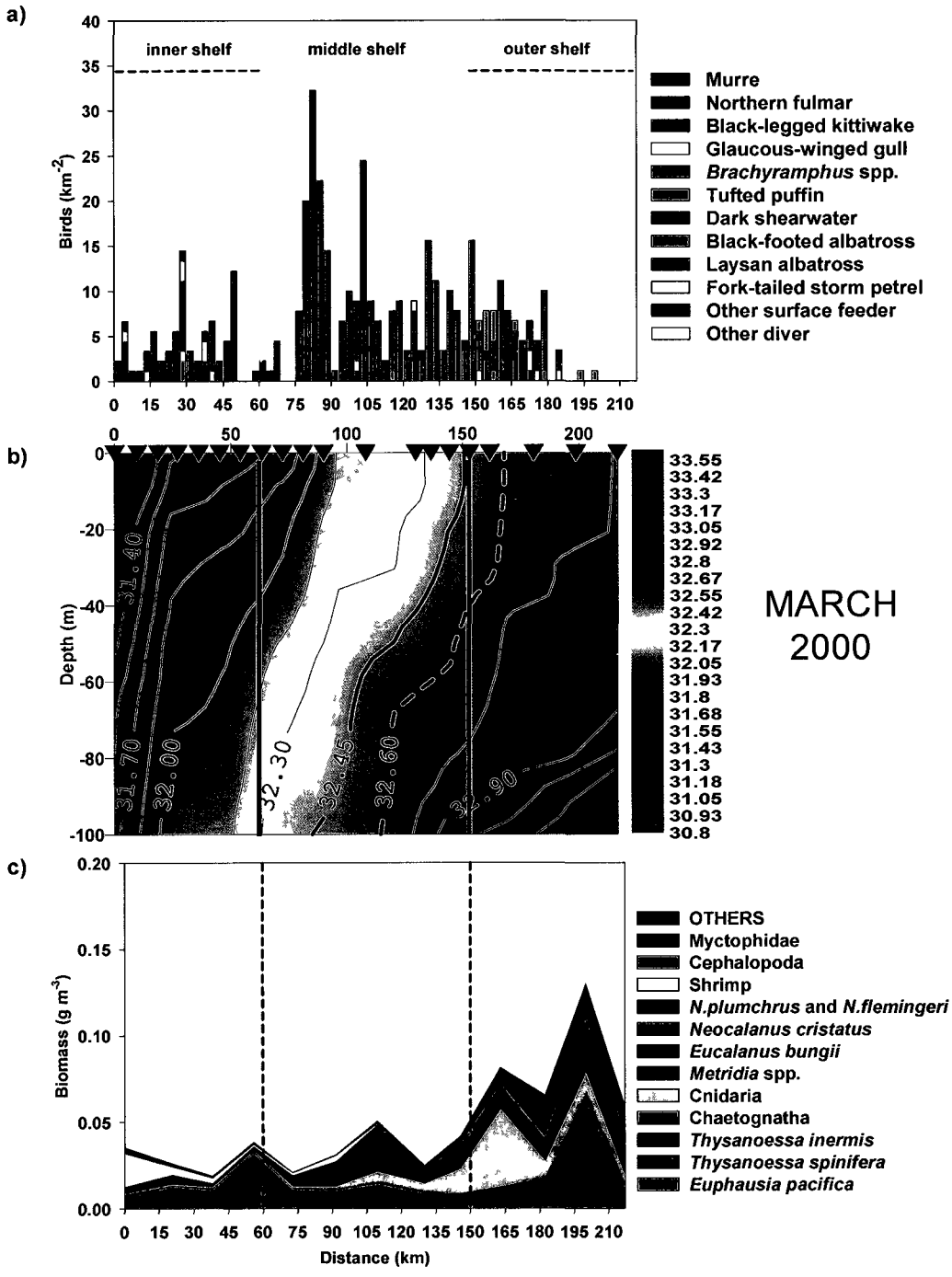

Figure 2.6. March 2000 (HX228), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

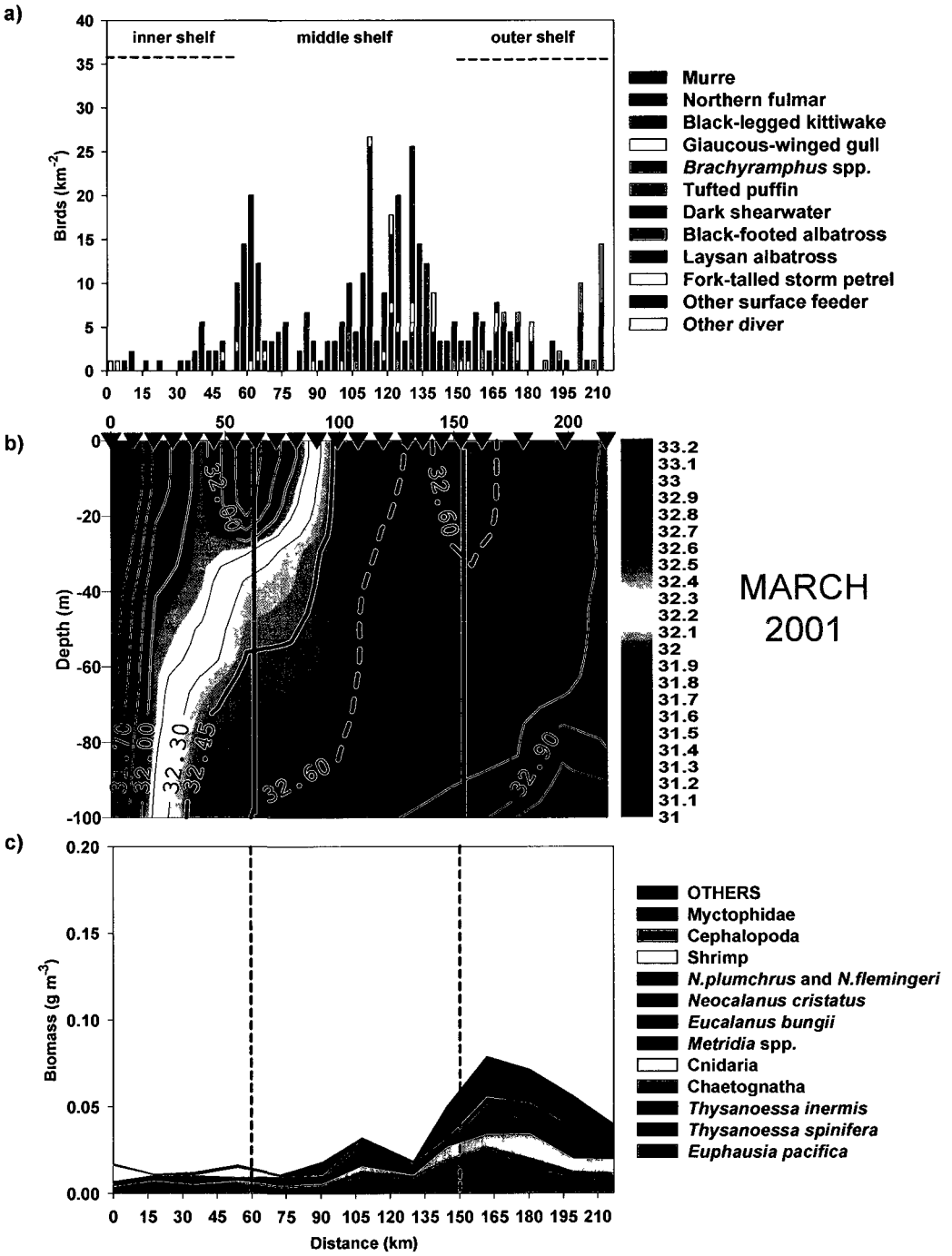

Figure 2.7. March 2001 (HX239), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

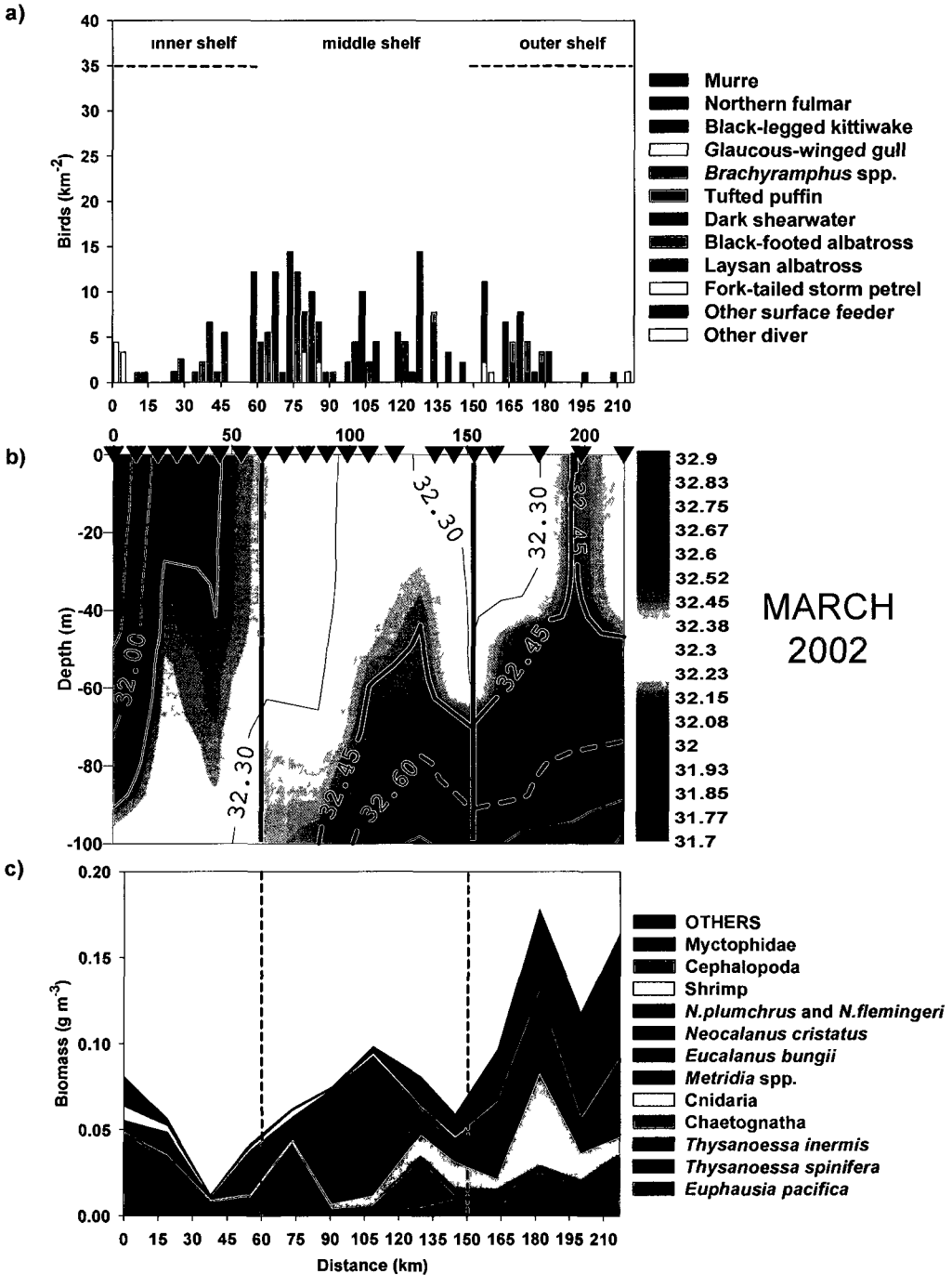

Figure 2.8. March 2002 (HX254), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

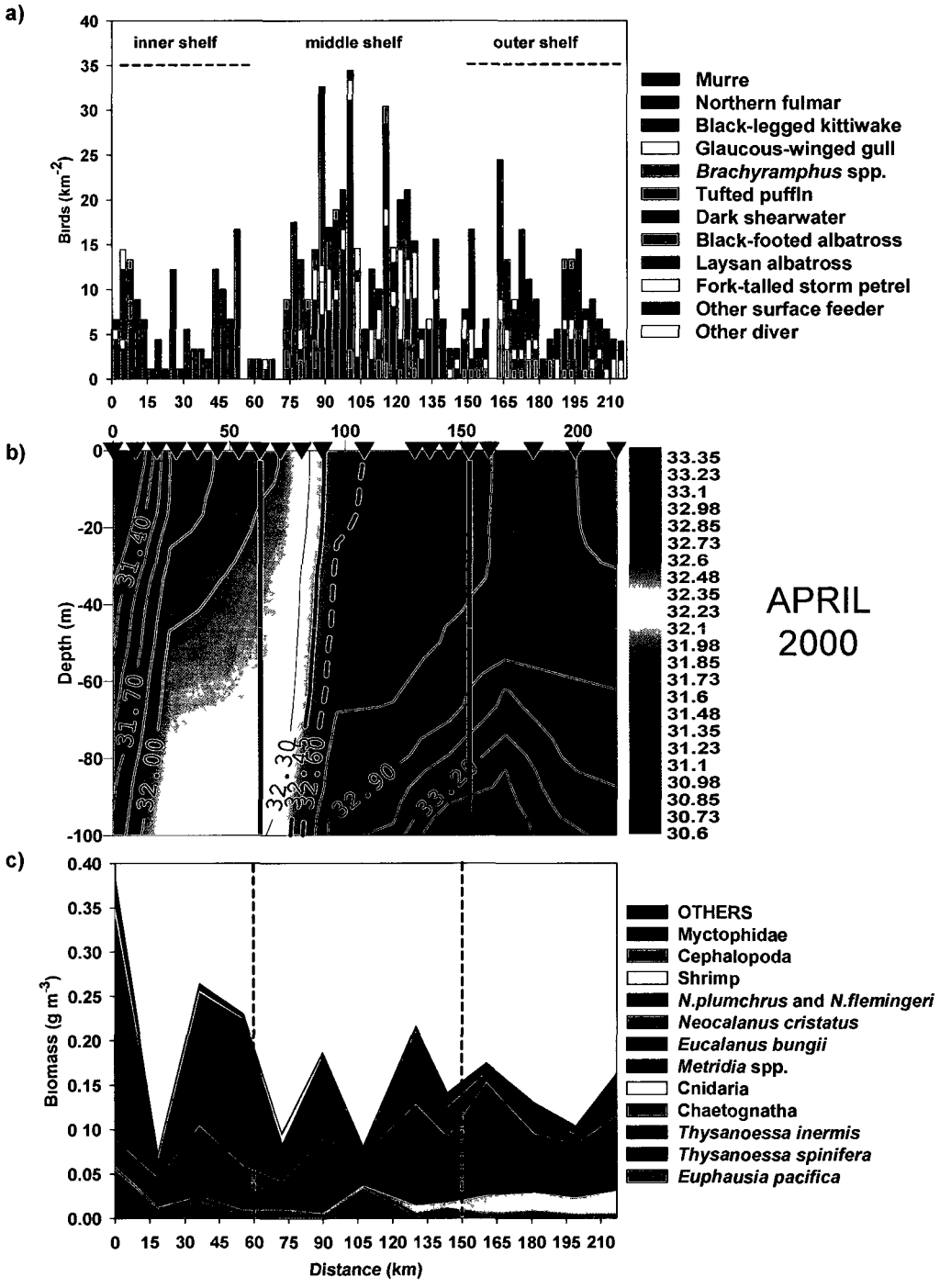

Figure 2.9. April 2000 (HX230), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

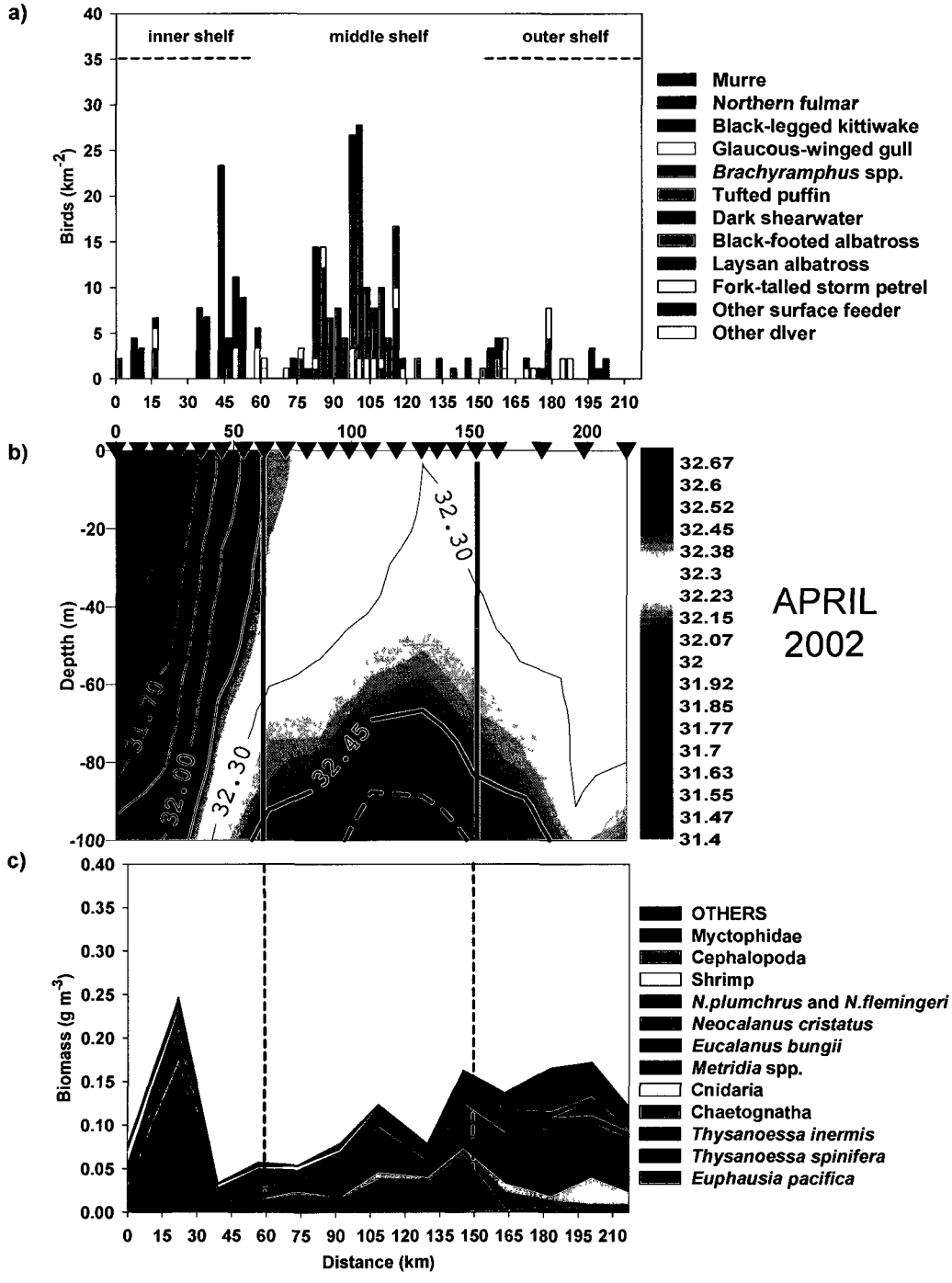

Figure 2.10. April 2002 (HX257), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

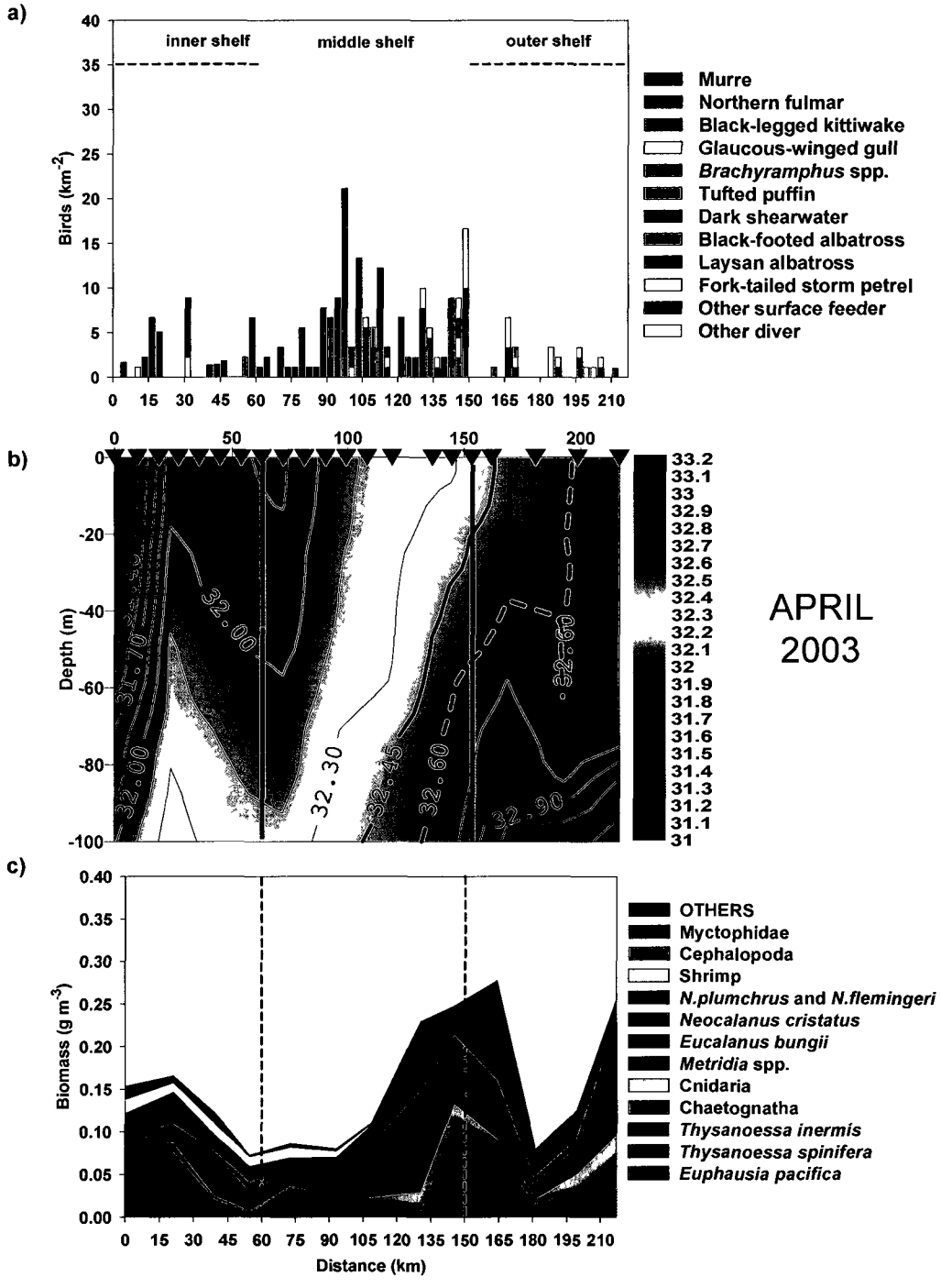

Figure 2.11. April 2003 (HX270), seabird abundance (a), salinity (b) and zooplankton biomass (c) along the Seward line. Filled triangles indicate station locations.

CHAPTER 3. Climate-related variability in abundance of mesozooplankton in the northern Gulf of Alaska 1998-2009[4]

Abstract

Data are presented on the inter-annual changes of zooplankton abundance in relation to water mass properties in the northern Gulf of Alaska. At-sea surveys were undertaken during the month of May from 1998 to 2009 to collect data on zooplankton abundance and water mass properties. Significant changes in temperature, salinity and zooplankton abundance were identified during this period. *Thysanoessa inermis* and *Calanus marshallae* had increased abundances in years when there was a strong phytoplankton spring bloom preceded by anomalously cold winters. *Pseudocalanus* spp., *Neocalanus plumchrus/N. flemingeri*, *Euphausia pacifica* and *Oithona* spp. were more resilient to relatively high mean water temperatures. High zooplankton abundances in years of substantial cross-shelf mixing suggest that iron and nutrient transport between the shelf and oceanic domains are essential for sustaining high zooplankton populations via phytoplankton blooms. The abundance of zooplankton in the northern GOA is highly influenced by advective processes and changes in temperature. Further understanding of biological and physical mechanisms that control the GOA ecosystem are of major

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[4] Sousa L., Coyle K., Weingartner T., (2011) Climate-related variability in abundance of mesozooplankton in the northern Gulf of Alaska 1998-2009. Prepared for submission in *Marine Biology*

importance to predict the response of zooplankton communities to environmental changes.

Keywords: zooplankton, temperature, salinity, inter-annual, advection, neritic, oceanic

Introduction

The northern shelf of the Gulf of Alaska (GOA) is a rich and diverse ecosystem, which sustains a number of important fisheries resources such as crustaceans, salmon, halibut, pollock and sablefish (Ware and McFarlane 1989, Willette et al. 2001, Weingartner et al. 2002). Mesozooplankton (0.1-2 cm body length) are the trophic link between these fisheries target species and microplankton (primary producers and microheterotrophs) (Sigler et al. 2001, Armstrong et al. 2005, Dagg et al. 2006, Liu et al. 2008). Substantial changes in fisheries populations have occurred in the GOA. In the mid-1970s, salmon and ground fish populations increased, while crab and shrimp populations decreased, and these changes corresponded to a strong regime shift in 1976-77 (Francis and Hare 1994, Mantua et al. 1997, Anderson and Piatt 1999). Later in the 1980s, marine mammal and seabird populations also declined, while the ground fish populations continued to increase (Merrick et al. 1987; Hatch and Sanger 1992; Springer 1998). These variations suggest that the GOA is susceptible to climate variations, although there is no clear understanding of the mechanistic links between climate variability and ecosystem change. In this study, I investigate the inter-annual variation in

zooplankton abundance and its association with water mass properties in the northern GOA from 1998-2009.

The zooplankton community in the northern GOA is mainly composed of copepods, euphausiids, chaetognaths, pteropods, larvaceans and cnidarians (Coyle and Pinchuk 2003). The biomass in the zooplankton community is usually dominated by large oceanic copepods, such as *Neocalanus cristatus, N. plumchrus, N. flemingeri* and *Eucalanus bungii*, which are responsible for the annual biomass peak during spring and early summer (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005). This seasonal biomass peak is related to life cycle timing of these dominant copepod species, which over-winter in deep waters below the pycnocline and migrate above the pycnocline in spring and early summer to feed and complete their somatic growth (Miller and Clemons 1988; Tsuda et al. 1999; Kobari and Ikeda 2001a). Subsequently, the rapid summer decline in biomass occurs mainly because these four species migrate to diapause in deep waters (Kobari and Ikeda 2001b; Tsuda et al. 2004; Coyle and Pinchuk 2005). Conversely, small neritic copepods, such as *Calanus marshallae, Metridia pacifica, Pseudocalanus spp.* and *Oithona spp.*, are the most populous species in the zooplankton community, which have an annual abundance peak in summer. Therefore, the biomass and abundance peaks in zooplankton species in the GOA are mainly represented by oceanic and neritic copepod species, respectively (Coyle and Pinchuk 2003).

The northern GOA is a very dynamic environment, and has a complex bathymetry with many canyons, troughs and a deep shelf (Weingartner et al. 2005). During fall and

winter, intense westward alongshore winds cause onshore Ekman transport and coastal downwelling on the shelf. During spring and summer downwelling diminishes as winds relax (Stabeno et al. 2004; Weingartner et al. 2005). The main currents in this region are the Alaska Coastal Current (ACC), which flows westward within 20–50 km of the coast (Royer 1982; Weingartner et al. 2005), and the Alaska Current offshore Kodiak Island, which narrows and intensifies to become the Alaskan Stream, a western boundary current of the Subarctic Gyre (Reed 1984; Reed and Stabeno 1989).

Zooplankton species may respond differently to changes in temperature and food concentration, and their abundance may also change as a result of vertical and cross-shelf mixing that may affect dispersal of organisms in the water column (Coyle and Pinchuk 2005; Mackas and Coyle 2005; Pinchuk et al. 2008). Therefore it is important to understand how zooplankton species respond to changes in water mass properties. This study examines the relationship between the abundance of sixteen zooplankton taxa and water mass properties, to determine if inter-annual changes in their abundance are related to water mass properties in the northern GOA.

Methods

Study area

As part of the Global Ocean Ecosystems Dynamics (GLOBEC) Long Term Observation Program (LTOP) in the northern GOA, surveys were conducted along the

Seward line (~220 km) during May from 1998-2009 (Figure 3.1). Rough weather precluded a complete coverage of the Seward line in 2008; therefore, this survey year was not included in my analyses. Data from May were chosen for analysis because zooplankton biomass peaks in May (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005) and because continued sampling in May has provided an unterrupted time series from 1998 to the present.

The study area can be divided into three zones: inner, middle shelves and oceanic domain (Figure 3.1). The inner shelf is highly influenced by freshwater runoff, and occasionally high salinity oceanic waters are advected onto the middle shelf, which has a mixture of neritic and oceanic waters (Coyle and Pinchuk 2005). The oceanic domain has high salinity waters from the oceanic environment, and can be subject to the activity of mesoscale anticyclonic eddies that move along the shelf slope (Okkonen et al. 2003; Janout et al. 2009). The shelf in this area is broad (160 km wide) and deep, with bottom depths exceeding 150 m. Irregular bathymetry characterizes the shelf; water shoals from 250 m on the inner shelf to 150 m in the middle shelf before deepening again (Figure 3.1).

Data collection

Large zooplankton and micronekton were collected with a 1 m^2 Multiple Opening/ Closing Net and Environmental Sampling System (MOCNESS) (Wiebe et al. 1976) with 500 μm mesh nets. The nets were fished at night and five oblique samples

were collected in 20-m increments from 100 m depth to the surface. The small-bodied zooplankton component was sampled with a 25-cm diameter CalVET system (CalCOFI Vertical Egg Tow; Smith et al. 1985) having 150- μm mesh nets. Each net was equipped with General Oceanics flowmeters in the mouth of the nets to monitor volume filtered. The net was fished at daytime and vertically from 100 m depth to the surface. Zooplankton samples were taken at 13 stations spaced 18 km apart along the Seward line (Figure 3.1). Samples were preserved in a 10% formalin seawater solution and stored for later analysis. All animals in the samples were sorted and identified to the lowest taxonomic category possible, abundance estimates were calculated following the methods of Coyle and Pinchuk (2005), and results were integrated for the upper 100 m of the water column.

Conductivity-temperature-depth (CTD) profiles were collected from surface to bottom at 1 m increments using a Seabird model 911 Plus fitted with conductivity, temperature and fluorescence sensors (Weingartner et al. 2005). Nineteen stations at ~8 km intervals were sampled along the shelf and slope, and 3 stations at ~18 km intervals were sampled off the shelf break (Figure 3.1). Mean temperature, salinity and sigma-t were calculated by averaging data from the upper 100 m. Pycnocline depths were determined by calculating the depth of greatest change in sigma-t through the water column. Average upper and lower temperatures, salinities and sigma-t were calculated above and below the pycnocline. In addition, the stratification parameter, the energy

required to redistribute the water-column mass by complete vertical mixing (J m^{-3}), was computed (Simpson et al. 1977; Fiedler et al. 1998).

Data analysis

Inter-annual variation

The data collected in this study were used to determine the relationship between mean zooplankton abundance and water mass properties and to characterize their inter-annual variations in the northern GOA. I tested the alternative hypothesis that mean zooplankton abundance and water mass properties are different between years, in opposition to the null hypothesis that zooplankton abundance and water mass properties are not different between years. I developed these hypotheses to examine if northern GOA zooplankton abundance is significantly different in years when water mass properties are significantly different.

Analysis of variance (ANOVA) was used to test the alternative hypothesis that mean zooplankton abundance, salinity, temperature, pycnocline depth and stratification parameter were different among (Zar 1999). The most abundant taxonomic groups in our surveys were selected for data analysis (1-*Pseudocalanus* spp.; 2-*Oithona* spp. 3-*Acartia* spp., 4-*Metridia* spp., 5-*Calanus marshallae*, 6-*Neocalanus plumchrus* and *Neocalanus flemingeri*, 7-*Neocalanus cristatus*, 8-*Eucalanus bungii*, 9-Calanoid nauplii, 10-*Euphausia pacifica*, 11-*Thysanoessa inermis*, 12-*Thysanoessa spinifera*, 13-Pteropoda,

14-Chaetognatha, 15-Larvacea, 16-Cnidaria). Zooplankton analyses were performed using STATISTICA 6 software. Zooplankton abundance was power transformed to stabilize the variance and tests were considered significant if $p \leq 0.05$. Tukey's test was used to identify which years had significantly different mean zooplankton abundance. ANOVA and Tukey's test were also used to test for differences in zooplankton abundance, salinity, temperature, pycnocline depth and stratification parameter among zones.

Model development

Generalized additive model regressions (GAM) (Hastie and Tibshirani 1990, Wood 2006) were used to investigate the relationship between zooplankton abundance and water mass properties. GAM is a non-parametric regression method, which reduces the assumptions of normality and linearity inherent in linear regression and is comprised of a response variable, an additive predictor, and a link function that links the two components. A model with p explanatory variables has the following form:

$$g(\mu) = \alpha \sum_{j=1}^{p} f_j(x_j) \qquad \text{(Equation 3.1)}$$

Where μ is the mean of the response variable, α is a constant term, f_j are the non-parametric smoothing functions of the explanatory variables x_j, and g is the link function.

In this study the response (or dependent) variables in the GAM's were mean abundance of each zooplankton taxon per station. Therefore, an example of the link function $g(\mu)$ in Equation 3.1 would be: *g (mean abundance of Calanus marshallae)*. The predictor (or independent) variables in the GAM's were the mean value of water mass properties per station. Therefore, an example of $f_j(X_j)$ in Equation 3.1 would be: f_j *(mean temperature)* + f_j *(mean salinity)*. Zooplankton abundance was power transformed and GAM's were run using the mgcv library in R, version 2.11.1 (Wood 2004), with a gaussian family (normal distribution with an identity link function), and cubic regression splines as the smoothing function of predictor variables. For each taxon, a subset of predictor variables (water mass properties) that produced the best-fit models was selected using generalized cross validation (GCV) methods (Wood 2006). The GCV is a measure of the predictive error of the model and takes into account the fit and also the model complexity. Significance of the predictor variables was assessed by using Chi-square statistics calculated by R (R Development Core Team 2009). In addition, partial regression plots showing the additive effect of each predictor variable on the abundance of each zooplankton taxa were examined for linearity, significance and positive and negative effect. Residuals from best-fit models were checked for the assumption of independence and identical distributions. The resulting best-fit models were used to indicate which predictor variables may have an important effect on the abundance of each species.

Results

Inter-annual variation

ANOVA results including years (1998-2009) and "zones" (inner and middle shelves, and oceanic domain; Figure 3.1) were the same as the results for ANOVA including years only; therefore, only the latter are included in this paper. Significant inter-annual changes were observed in water mass properties and zooplankton abundance in May along the Seward line in the northern GOA (Tables 3.1, 3.2). Relatively high (> 6.00°C) mean temperatures above the pycnocline enhanced stratification (> 50 J m^{-3}) of the water column in 1998, 2000, 2003, 2005, and 2009 (Figures 3.2a, 3.3a). Mean temperatures below the pycnocline and mean temperatures in the upper 100 m were relatively higher (> 6.00°C) in 1998, 2003 and 2005, and lower (≤ 5.00°C) in 2002, 2007 and 2009 (Figure 3.2a, Table 3.1). Mean salinities in the upper 100 m and mean salinities above and below the pycnocline were relatively lower (< 32.20) in 2004 and 2005, and higher (> 32.20) in 1999, 2000 and 2001(Figure 3.2b, Table 3.1). Highest abundances of dominant copepod species (*Pseudocalanus* spp., *Oithona* spp., calanoid nauplii, *Neocalanus plumchrus* and *N. flemingeri*, and *Metridia* spp.) occurred in 1998, 2000, 2002, 2005 and 2006 and lowest in 1999 and 2001 (Table 3.2, Figure 3.4). However, euphausiids showed a partially different trend, with abundance peaks of *Euphausia pacifica* in 1999 and 2005, *Thysanoessa inermis* in 2001, 2002, 2007 and 2009, and *Thysanoessa spinifera* in 2000, 2001 and 2009 (Table 3.2, Figures 3.4j, 3.4k, 3.4l).

Interpreting GAM results

Results from GAM's are displayed as a set of partial regression plots, which show the best fitting smooth for the explanatory variable on the response variable. Results of GAM output for *Calanus marshallae* are explained here in detail to assist in interpretation of the results in this study. Table 3.3 shows that the best fit model for predicting the mean abundance of *Calanus marshallae* is:

$$g(C.marshallae) = \alpha + f(Lotemp) + f(UpSal) + f(LoSal)$$

(Equation 3.2)

Where *C. marshallae* is the mean abundance of *Calanus marshallae*, *LoTemp* is mean temperature below the pycnocline, *Upsal* is mean salinity above the pycnocline, and *LoSal* is mean salinity below the pycnocline. This model explains 74% of the variance in the mean abundance of *Calanus marshallae* (Table 3.3). The added effect of each smoothed explanatory variable ($f(Lotemp) + f(UpSal) + f(LoSal)$) on the response variable ($g(C.marshallae)$) is shown in Figure 9 using partial regression plots. Two standard error bounds are shown around the best fitting smooth curve. Therefore, the relative importance of each explanatory variable is reflected on the y-axis. Along the x-axis a "rug" is included as a set of tick marks, which indicate the locations for the data points used to compute the GAM smooth curve. The rug shows where the data are dense and where they are sparse. Mean salinity above the pycnocline had a strong negative effect on *C. marshallae* abundance while mean salinity below the pycnocline and mean

temperature below the pycnocline had a weaker effect on *C. marshallae* abundance (Figure 3.7, Table 3.3).

GAM results

Best-fit GAM's showed significant relationships between zooplankton abundance and water mass properties. Salinity had a significant effect on the abundance of 13 out of 16 zooplankton taxa and temperature had a significant effect on 10 taxa. Pycnocline depth did not have a significant effect on the abundance of any zooplankton taxa, while the stratification parameter had a significant effect on only two out of 16 zooplankton taxa (Table 3.3).

Pseudocalanus spp. and *Acartia* spp. abundances were negatively associated with mean salinity in the upper 100 m (Figures 3.5, 3.6). *Eucalanus bungii* and *Neocalanus cristatus* were positively associated with mean salinity in the upper 100 m (Figures 3.6, 3.7). Mean salinity in the upper 100 m was negatively associated with *Neocalanus plumchrus* and *Neocalanus flemingeri* abundance when salinity values were approximately > 32.25 (Figure 3.7). Mean salinity above the pycnocline, within the 31.60 to 32.75 range, had a significant effect on the abundances of calanoid nauplii and *Metridia* spp., which were negatively associated with salinities >32.50 and > 32.60, respectively (Figures 3.6, 3.7). *Oithona* spp. was associated with mean salinity above the pycnocline, within the 32.00 to 32.75 range, and had a negative response to salinities > 32.30 (Figure 3.5). Mean salinity above the pycnocline, within the 31.50 to 32.75 range,

had a significant effect on the abundance of larvaceans and cnidarians, such that the former had an oscillating response within this range and the latter was positively associated with salinities > 31.75 (Figure 3.9). *Thysanoessa spinifera* were associated with a narrow range (32.25-32.50) in mean salinity below the pycnocline (Figure 3.8).

Mean temperature in the upper 100 m had a weak effect on the abundance of *Eucalanus bungii*, a negative effect on the abundance of *Thysanoessa inermis* and a positive effect on pteropods (Figures 3.6, 3.8). Furthermore, *Pseudocalanus* spp. and *Euphausia pacifica* had a positive response to mean temperatures in the upper 100 m between 5.75 and 6.25°C and between 4.50 and 5.50°C, respectively (Figures 3.5, 3.8). Mean temperature above the pycnocline had a weak effect on the abundance of calanoid nauplii and a positive effect on the abundance of *Oithona* spp. when temperatures were 6.00-7.00°C (Figures 3.5, 3.6). In addition, mean temperature below the pycnocline was positively associated with the abundance of Chaetognatha and Cnidaria. Finally, *Pseudocalanus* spp. and pteropods were associated with stratification parameters near 60 ($J\ m^{-3}$).

Discussion

This study showed a wide range of associations between zooplankton abundance and water mass properties, suggesting complex interactions of abiotic and biotic factors that influence zooplankton distribution and abundance in the northern GOA. Mixing processes can influence the distribution of zooplankton species, such that oceanic species

are advected into the coastal habitat and neritic species towards the slope (Coyle and Pinchuk 2005; Mackas and Coyle 2005; Pinchuk et al. 2008). These processes include seasonal changes in cyclonic winds and Ekman transport and interactions of currents with the complex coast and bathymetry that can generate eddies and meanders that enhance cross-shelf transport of water masses (Okkonen et al. 2003; Weingartner et al. 2005; Janout et al. 2009). Species that are abundant in the upper mixed layer such as *Neocalanus plumchrus and N. flemingeri* are likely to be advected onshore by Ekman transport, while species that are abundant below the mixed layer such as *N. cristatus* and *Eucalanus bungii* are not. Taxa that undergo diel vertical migration such as *Metridia* spp. and euphausiids will be influenced by Ekman transport at night and subsurface flow during the day. In addition, many of the zooplankton in the GOA are herbivorous and depend on high primary productivity. The GOA basin is a nitrate-rich-iron-limited environment, but the ACC is iron-rich and nitrate is limited in late spring and summer (Childers et al. 2005; Strom et al. 2007; Wu et al. 2009). Physical processes that enhance cross-shelf mixing should elevate primary production and may result in higher zooplankton abundance (Coyle and Hermann 2010). Therefore, the intensity and timing of these abiotic and biotic variables may affect zooplankton abundance in the northern GOA.

Inter-annual variability and zooplankton associations with water mass properties

Euphausiids

Thysanoessa inermis was abundant in 2001, 2002, 2007 and 2009 (Figure 3.4j). *Thysanoessa inermis* is mostly herbivorous, releases eggs only once per spawning season, and relies on lipid storages to overwinter (Falk-Petersen 1981; Falk-Petersen et al. 1981; Pinchuk and Hopcroft 2006). Furthermore, this species is characteristic of the shelf environment and may benefit from enhanced primary productivity during the spring bloom (April-May) (Lu et al. 2003; Coyle and Pinchuk 2005; Pinchuk et al. 2008). Previous studies suggest that increases in the abundance of *T.inermis* are largely dependent on body condition before the spring bloom and that high chlorophyll *a* concentrations are required to renew energy requirements after spawning (Falk-Petersen 1981; Falk-Petersen et al. 2000). Hence, cold conditions in winter and early spring would lower metabolic rates and result in slow consumption of lipid stores and therefore stronger body condition (Pinchuk et al. 2008). Temperatures during the winters of 2001-2002, 2006-2007, 2007-2008 and 2008-2009 were anomalously low on the inner shelf in the northern GOA, with mean water column temperatures < 5.00°C compared to mean water column temperatures of ~6.00°C in the other winters (1998-2001; 2002-2006) (Janout et al. 2010; Weingartner unpublished data). High abundances of *T.inermis* in 2001, 2002, 2007 and 2009 after previous years of anomalous low temperature support the concept that cooler temperatures contribute to increased abundance of this species.

Euphausia pacifica is a subtropical-temperate species and is close to the northern boundary of their distribution in the northern GOA, which is dominated by subarctic species (Brinton 1962; Mauchline and Fisher 1969). Lowest abundances of *E. pacifica* occurred in 2002, 2007 and 2009 when mean temperatures in the upper 100 m were extremely low (Figures 3.2a, 3.4k). High abundances occurred in 1999 when mean temperature in the upper 100 m was similar to the overall mean (5.70 °C), and in 2005 when temperatures were significantly higher than the overall mean (Figures 3.2a, 3.4k; Table 3.2). GAM results suggest a temperature threshold so that *E. pacifica* populations increase until mean water temperatures in the upper 100 m are above 5.50 °C; beyond this temperature value there is little consistent effect on their abundance (Figure 3.8). Lowest temperatures below the pycnocline were above 5.50 °C between 2003 and 2006 (Figure 3.2a), suggesting that if temperatures are above 5.50 °C, some other limiting factor is more likely to affect *E. pacifica* populations, but below 5.50 °C temperature may be the dominant controlling variable in this area.

Copepods

Pseudocalanus spp. and *Neocalanus plumchrus/N. flemingeri* were the only copepods that showed elevated abundances in 1998. The 1997-1999 period included an El Nino event (1997-1998) followed by a La Nina event (1998-1999). Higher temperatures and lower salinities occurred in 1998, and lower temperature and higher salinity in 1999 (Figures 3.2a, 3.2b) (Weingartner et al. 2005). In 1998 the

phytoplankton spring bloom occurred earlier and was weaker compared to 1999 (Pinchuk et al. 2008). *Pseudocalanus* spp. are abundant in the inner shelf and *N. plumchrus/N. flemingeri* are abundant throughout the shelf and slope in the northern GOA. Both *Pseudocalanus* spp. and *N. plumchrus/N. flemingeri* are able to feed on a wide range of particle sizes (Peters 1983; Dagg et al. 2006; Peters et al. 2006; Liu et al. 2008). The high abundances of *Pseudocalanus* spp. and *N. plumchrus/N. flemingeri* in 1998 suggest that the ability of these species to feed on smaller particle sizes may enable them to take advantage of the early spring bloom and to have increased growth during this warm period.

Other taxa

Pteropods and chaetognaths were positively associated with mean temperature in the upper 100 m and below the pycnocline, respectively (Figures 3.8, 3.9). Increased abundance of chaetognaths has been associated with increased temperatures in the southeastern Bering Sea and in the Kuroshio region in the western GOA (Nakata and Koyama 2003; Baier and Terazaki 2005). Furthermore, when water temperatures are higher later in the year (July-October), chaetognaths reach their highest abundance and biomass (Coyle and Pinchuk 2003). The relatively higher abundances of chaetognaths in 2003 when mean temperatures below the pycnocline were high suggest that they may increase in abundance during warm conditions (Figure 3.4n). Many chaetognath species are known to undergo diel vertical migration; however, smaller individuals can remain at

the surface, therefore being exposed to more mixing within the mixed layer (Brodeur and Terazaki 1999). The broad spectrum of species within Chaetognatha is likely to have differing physiological tolerances to conditions in this area, such that some species may do better in some years than others, depending on those tolerances. While grouping species may indicate broad overall trends for the group as a whole, large confidence intervals are expected because they are species groups and not single species (Figures 3.4n). High abundances of pteropods in 1998, 2003, 2005 and 2006 occurred when mean temperature in the upper 100 m and stratification parameter were highest (Figures 3.4m, 3.3a), except for 2006 when water column properties were average. Many Pteropods are passive feeders that capture food using a spherical mucous web several times the size of their body (Gilmer 1972; Gilmer and Harbison 1986) and may benefit from a more stable water column given that intense mixing may damage the mucus web and make it difficult to capture food.

Model analyses on selected species and their habitat - GAMs

Variations in the abundance of *Pseudocalanus* spp. include the response of several species (*P. minutes*, *P. multani*, *P. newmani*, *P. mimus*) that are part of this genus and occur in the northern GOA. GAM's showed the association of *Pseudocalanus* spp. with neritic waters which were warm, stratified and had low salinities (Figure 3.5). Their abundance was highest in years of low salinity, high temperature and stratification parameter (Table 3.1). However, peak abundance of *Pseudocalanus* spp. occurred in

2000 when salinity was elevated (Figure 3.2b) and intense eddy activity occurred, with small and large eddies propagating across the shelf (Coyle and Pinchuk 2005). The clear negative trend of *Pseudocalanus* spp. populations with salinity detected by the GAM's and highest abundance values in 2000 when salinity was high, indicates that the GAM's extracted the general trend in the data, which may not hold for individual years.

Calanus marshallae is a neritic species and is most abundant in the upper 40 m (Coyle and Pinchuk 2005). It was most abundant in 2005 and 2006 when mean salinity above the pycnocline was low (Figures 3.4g and 3.2) and the 32.25 isohaline extended to the end of the Seward line and the 32.50 isohaline extended to the middle shelf (GAK 6) (Figures 3.10, 3.1). Salinities < 32.25 and > 32.50 are characteristic for the ACC and oceanic waters, respectively (Weingartner et al. 2005). This suggests that enhanced cross-shelf mixing of coastal waters offshore, within the Ekman layer, elevates *C. marshallae* concentrations. The cross-shelf advection in the Ekman layer promotes production by mixing low-nitrate high-iron coastal water with low-iron high-nitrate oceanic water. *Calanus marshallae* is a herbivorous species and is likely to benefit from increased primary production (Baier and Napp 2003).

Neocalanus cristatus and *Eucalanus bungii* had a positive response to mean salinity in the upper 100 m, reflecting their association with oceanic waters (Figures 3.6, 3.7). *Eucalanus bungii* showed inter-annual variation in abundance. Conversely, there were no significant inter-annual differences in the abundance of *N. cristatus*. GAM results suggest that *Eucalanus bungii* abundance increases until salinity is about 31.50

and is fairly constant afterwards. Thus, they are tolerant of a broader spectrum of conditions and are likely to occur at more stations along the Seward line (Figures 3.6, 3.1). However, *N. cristatus* populations do not peak until salinity is about 32.30 (Figure 3.7). This suggests that a large section of the study area would have to have elevated salinity to result in consistently higher *N. cristatus* populations, so changes in the abundance of this species are more likely to have broader confidence intervals. This study suggests that these animals may be intolerant of the lower salinity associated with the ACC.

There was a sharp decrease in calanoid nauplii, *Oithona* spp. and *Metridia* spp. abundance when salinity exceeded 32.50 in the upper mixed layer (Figures 3.5, 3.6, 3.7). Calanoid nauplii can be from any calanoid species and differences in species composition are likely to contribute to broader confidence intervals and standard errors (Figures 3.4d, 3.6). *Oithona* spp. and *Metridia* spp. on the other hand, are dominated by one species each (*Oithona similis and Metridia pacifica*, respectively) (Coyle and Pinchuk 2003; Coyle and Pinchuk 2005), so differences in species composition are less likely to affect confidence intervals and standard errors (Figures 3.4b, 3.4h, 3.5, 3.7). High chlorophyll *a* concentrations associated with eddy activity may have contributed to the high abundance of these taxa in 2000 and 2002 (Coyle and Pinchuk 2005; Janout et al. 2009). In addition, high abundances of calanoid nauplii occurred in years of low salinity and moderate temperature (Figures 3.2a, 3.2b, 3.4d). Low abundances of calanoid nauplii and warmer temperatures in 2003, relative to other years, may be partially explained by

the cruise date (23-28 May, 2003) being almost three weeks later than the other cruises in our study. Warmer water temperatures in 2003 may also have contributed to early breeding of copepods, which could help explain their low abundance in 2003.

Neocalanus plumchrus/N. flemingeri were abundant in 1998, 2002 and 2006 when the 32.25 isohaline extended to the end of the Seward line (1998, 2006) and to the shelf break (GAK 9, 2002), and the 32.50 isohaline extended to the inner (GAK 4, 1998,2002) and middle shelves (GAK 7, 2006) (Figures 3.1, 3.4i, 3.10). Salinities < 32.25 and > 32.50 are characteristic of the ACC and oceanic waters, respectively, which suggests that the Seward line was characterized by considerable cross-shelf mixing of oceanic and shelf water salinity. *Neocalanus plumchrus/N. flemingeri* are particle grazers and are predominantly herbivorous in coastal regions during the phytoplankton spring bloom. Their abundance appears to increase when mixing of iron-poor nutrient-rich oceanic water and nutrient-poor iron-rich shelf waters occurs. Wind and eddy activity often influence cross-shelf mixing and may contribute to enhanced primary production of chain-forming diatoms (Okkonen et al. 2003; Strom et al. 2007; Janout et al. 2009). These conditions may have contributed to the high abundances of *N. plumchrus/N. flemingeri* during this period.

In 2002 there was intense eddy activity along the Seward line (Okkonen et al. 2003; Coyle and Pinchuk 2005; Janout et al. 2009) and *Calanus marshallae*, *Neocalanus plumchrus/N. flemingeri* and *Thysanoessa inermis* had high abundances during this period (Figures 3.4g, 3.4i, 3.4j). *Calanus marshallae* occurs along the coast and south

towards Oregon in the upwelling region, where production is elevated and temperatures are lower. *Thysanoessa inermis* is a circumpolar arctic species that relies on lipid storage to overwinter (Falk-Petersen 1981; Peterson 1998; Baier and Napp 2003). Anomalously cold conditions in winter and early spring in 2002 (Janout et al. 2010) may have contributed to higher overwintering survival of *Calanus marshallae* and *Thysanoessa inermis*. *Neocalanus plumchrus/N. flemingeri* were likely unaffected by colder conditions in the upper 100 m, since they overwinter in deeper water (Miller and Clemons 1988) and perhaps differences in the timing and intensity of the spring phytoplankton bloom may have contributed to their elevated abundances in 2002.

Conclusions

The northern GOA has undergone significant variations in temperature, salinity and zooplankton abundance in the month of May from 1998-2009. The data indicate that very few species in the zooplankton community are able to maintain high abundances when water temperatures are high and there is an early and weak phytoplankton spring bloom. Furthermore, herbivorous species that depend on lipid reserves to overwinter (i.e., *Thysanoessa inermis*, *Calanus marshallae*) may undergo extreme declines in abundance if these conditions are preceded by warm winters. Species that are able to feed on a wide range of particle sizes (*Pseudocalanus* spp., *Neocalanus plumchrus/N. flemingeri*, *Euphausia pacifica*) and have a flexible diet (*Oithona* spp.) appeared to be more resilient to warmer conditions. High zooplankton abundances in years of

substantial cross-shelf mixing suggest that iron and nutrient transport between the shelf and oceanic domains are essential for sustaining high copepod populations through large phytoplankton blooms. The abundance of zooplankton in the northern GOA is highly influenced by advective processes and changes in temperature. Their complex life histories, vertical distribution patterns and habitat associations, have a major influence on the response of each taxon to changes in environmental conditions. Further understanding of biological and physical mechanisms that control the GOA ecosystem are of major importance to predict the response of zooplankton communities to environmental changes.

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Table 3.1. Differences in mean water mass properties: mean salinity (upper 100 m, MSal), mean salinity above the pycnocline (UpSal), mean salinity below the pycnocline (LoSal), mean temperature (upper 100 m, MTemp), mean temperature above the pycnocline (UpTemp), mean temperature below the pycnocline (LoTemp) (°C), pycnocline depth (PycDep) (m), and stratification parameter (StratPar) (J m^{-3}), by year along the Seward line in May 1998-2009

	Year										
Variable	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2009**
MSal	32.11	32.46	32.50	32.44	32.23	32.24	31.96	32.08	32.16	32.31	32.34
Tukey test	2004 < 1999 ≈ 2000 ≈ 2001;										
UpSal	31.81	32.33	32.26	32.29	32.10	32.04	31.76	31.72	31.92	32.17	32.02
Tukey test	2005 < 1999 ≈ 2001; 2004 < 1999										
LoSal	32.30	32.63	32.61	32.63	32.42	32.29	32.06	32.16	32.27	32.36	32.40
Tukey test	2004 < 1999 ≈ 2000 ≈ 2001; 2005 < 2001										
MTemp	6.70	5.59	5.95	5.589	4.92	6.74	5.74	6.19	5.91	4.97	4.69
Tukey test	1998 ≈ 2003 > 2005 > 1999 ≈ 2001 ≈ 2004 > 2002 ≈ 2007 ≈ 2009										
UpTemp	6.94	5.76	6.80	5.70	5.12	8.31	6.235	7.69	6.27	5.62	6.04
Tukey test	2003 ≈ 2005 > 1998, 2000 ,2001, 2002, 2003, 2004, 2006, 2007, 2009; 1998 > 2001, 2002, 2003, 2004, 2006, 2007, 2009; 2000 > 1999, 2001, 2002, 2007, 2009; 2004 ≈2006 ≈ 2009 > 2002,										

Table 3.1. Continued

	Year										
Variable	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2009**
LoTemp	6.52	5.52	5.640	5.49	4.90	6.26	5.51	5.98	5.69	4.80	4.50
Tukey test	1998 ≈ 2003 > 1999, 2000, 2001, 2002, 2004, 2005, 2006, 2007, 2009; 2005 > 1999, 2001, 2002, 2004, 2007, 2009; 1999 ≈ 2000 ≈ 2001 ≈ 2004 ≈ 2006 > 2002 ≈ 2007 ≈ 2009										
PycDep	41.77	53.15	31.46	55.85	57.77	25.62	40.69	17.54	30.62	33.46	18.31
Tukey test	2005 ≈ 2009 < 1999 ≈ 2001 ≈ 2002										
StratPar	59.92	37.87	60.35	39.11	36.39	58.77	42.94	69.68	43.40	26.50	59.08
Tukey test	2005 > 1999 ≈ 2001 ≈ 2002 ≈ 2004 ≈ 2006 ≈ 2007; 2000 > 1999 ≈ 2001 ≈ 2002 ≈ 2007; 1998 ≈ 2009 > 1999 ≈ 2002 ≈ 2007; 2003 > 2002 ≈ 2007										

Table 3.2. Comparison of zooplankton abundance (number m^{-3}) among years along the Seward line in May 1998-2009; Tukey test results

Species	Year
Pseudocalanus spp.	2000 > 1999, 2001, 2003, 2007, 2009; 2001 < 1998, 2000, 2002, 2004, 2005, 2006
Oithona spp.	2000 > 1998, 1999, 2001, 2002, 2003, 2007, 2009; 2004 ≈ 2005 ≈ 2006 > 2009; 2001 < all years
Acartia spp.	2005 > 1998, 2007, 2009; 2006 > 1998, 2007
Metridia spp.	2002 > 1999
Calanus marshallae	2006 > 1998, 1999, 2000, 2001, 2003, 2007, 2009; 2005 > 1999, 2000, 2001, 2003, 2007, 2009; 2002 ≈ 2004 > 2001
Neocalanus spp.	1998 ≈ 2006 > 1999, 2000, 2001, 2003, 2005, 2009; 2002 > 2000, 2001, 2003
Neocalanus cristatus	none
Eucalanus bungii	2006 > 1998, 1999, 2002, 2003, 2007, 2009; 1998< 2000, 2001, 2004, 2005, 2006
Calanoid nauplii	2005 > 1998, 2001, 2003, 2009; 2000 ≈ 2004 > 2001,2003,2009; 2001 < all years
Euphausia pacifica	1999 ≈ 2005 > 2002, 2007
Thysanoessa inermis	2009 > 1998, 1999, 2000, 2003, 2004, 2005, 2006; 2001 ≈ 2002≈ 2007 > 1998, 1999, 2003, 2004, 2005, 2006

Table 3.2. Continued

Species	Year
Thysanoessa spinifera	2001 > 1998, 2004, 2006; 2000 ≈ 2009 > 2006
Pteropoda	2005 > 1999, 2000, 2001, 2002, 2004, 2006, 2007, 2009; 2003 > 1999, 2000, 2001, 2002, 2004, 2007, 2009; 1998 ≈2006 > 1999, 2000, 2001, 2002, 2007, 2009; 2000 ≈ 2001 ≈ 2004 > 2007
Chaetognatha	2003 > 2009
Larvacea	2001 < 2002, 2004, 2005
Cnidaria	none

Table 3.3. Species zooplankton abundance (response variable μ, see Equation 3.1) and water mass properties (predictor variable *Xj*, see Equation 3.1) used in best-fit GAM models; black cells: variable contribution to model significant at $p<0.05$; gray cells: variable contribution to model insignificant at $p>0.05$; blank cells: variables absent from model; pos: variable effect significant and positive; neg: variable effect significant and negative

Species	**Water mass properties**								
	MTemp	**UpTemp**	**LoTemp**	**MSal**	**UpSal**	**LoSal**	**PycDep**	**StratPar**	**Deviance Explained (%)**
C. marshallae					neg				74.0
Pseudocalanus spp.	pos			neg					67.2
Pteropoda	pos								55.7
Oithona spp.									55.0
Calanoid nauplii									47.1
E. bungii				pos					46.5
Chaetagnatha			pos						39.7
Metridia spp.									39.3
Acartia spp.				neg					36.8
T. inermis	neg								34.7

Table 3.3. Continued

Species		Water mass properties								
		MTemp	**UpTemp**	**LoTemp**	**MSal**	**UpSal**	**LoSal**	**PycDep**	**StratPar**	**Deviance Explained (%)**
Larvacea						pos				33.9
N. cristatus					pos					29.3
E. pacifica		pos								28.6
Cnidaria				pos		pos				28.1
N. plumchrus and N. flemingeri					pos					20.2
T. spinifera							pos			20.0

"MTemp" = mean temperature in the upper 100 m; "UpTemp" = mean temperature above the pycnocline; "LoTemp" = mean temperature below the pycnocline; "MSal" = mean salinity in the upper 100 m; "UpSal" = mean salinity above the pycnocline, "LoSal" = mean salinity below the pycnocline; "PycDep" = pycnocline depth; "Stratpar" = stratification parameter

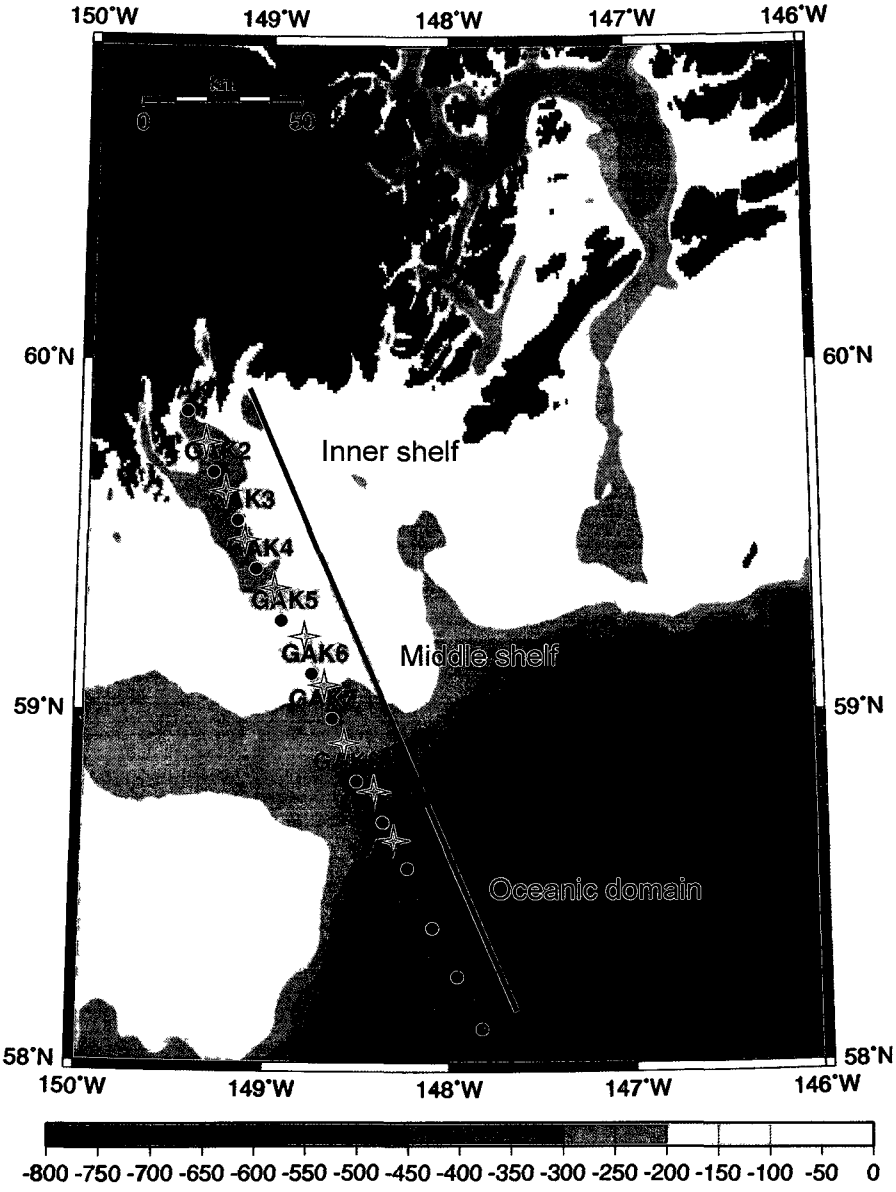
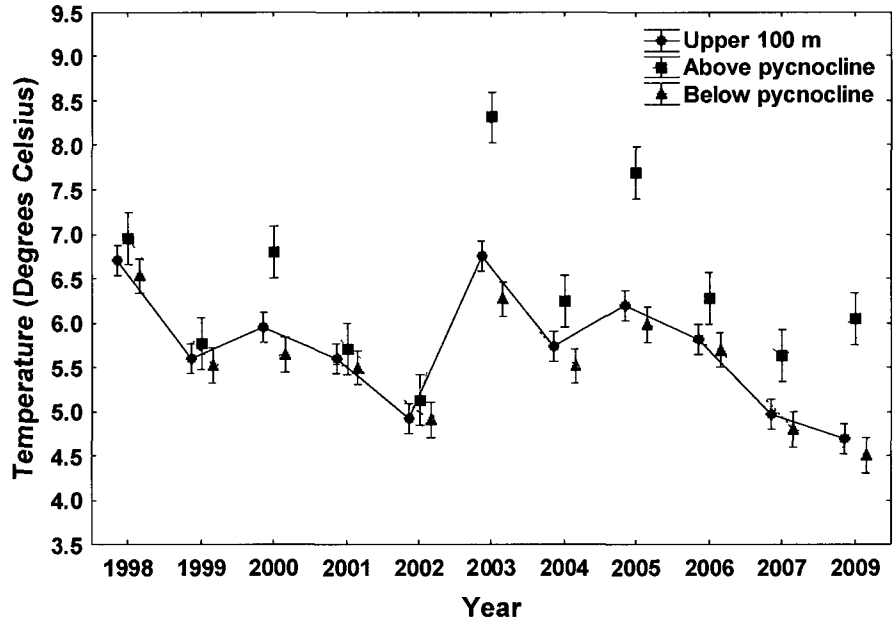


Figure 3.1. Station locations that were sampled in May (1998-2009) in the northern GOA along the Seward line (220 km); black dots represent stations where zooplankton and physical oceanography data were collected; stars represent stations where only physical oceanography data were collected. Colored lines indicate the three shelf zones (black-inner, red-middle, blue-oceanic) and scale bar indicates bottom depth (m).

a)



b)

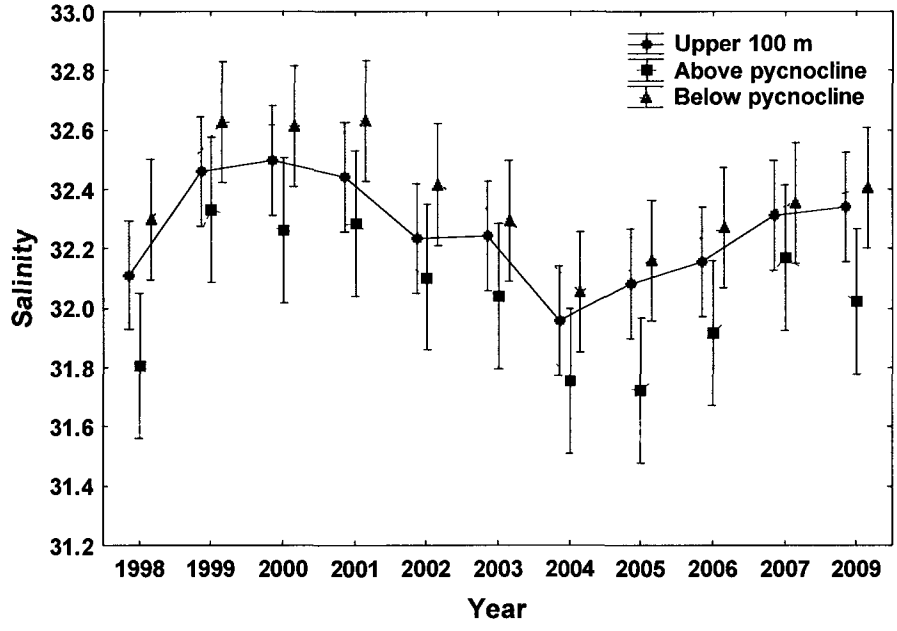
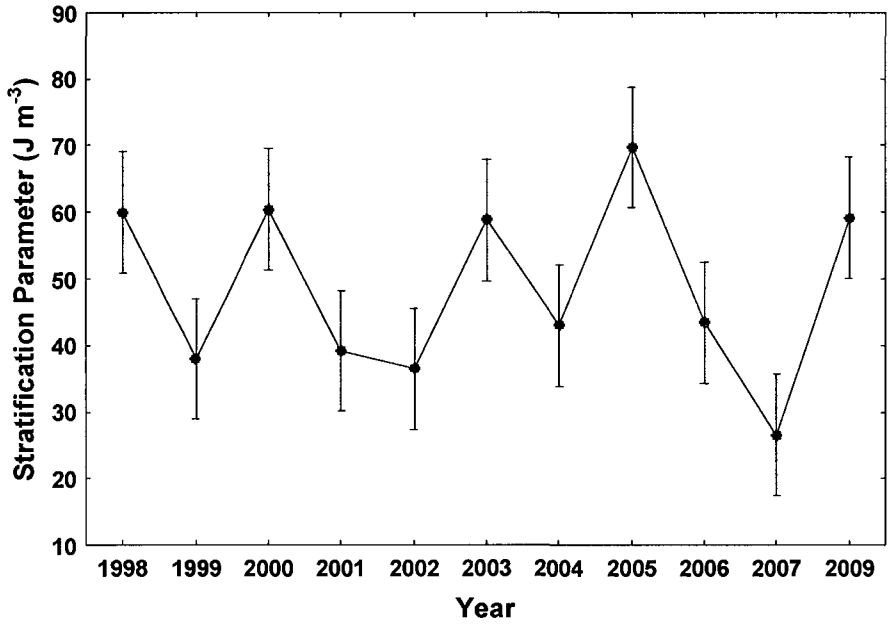


Figure 3.2. Annual changes in temperature (a), and salinity (b), above and below the pycnocline, and through the entire mixed layer (0-100 m) in May along the Seward line in the northern GOA 1998-2009; error bars are 95% confidence intervals

a)



b)

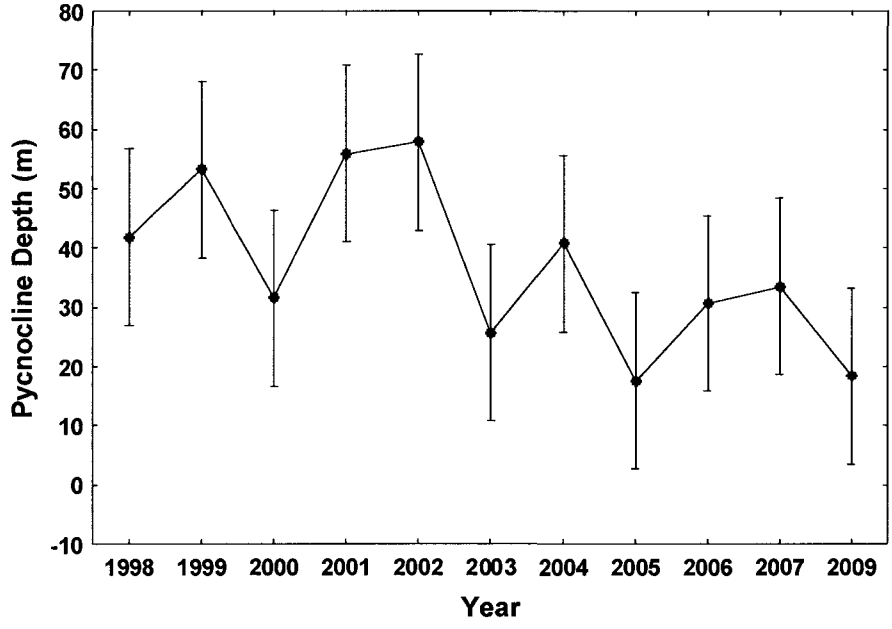


Figure 3.3. Annual changes in stratification parameter (a), and pycnocline depth (b) through the mixed layer (0-100 m) in May along the Seward line in the northern GOA 1998-2009; error bars are 95% confidence intervals

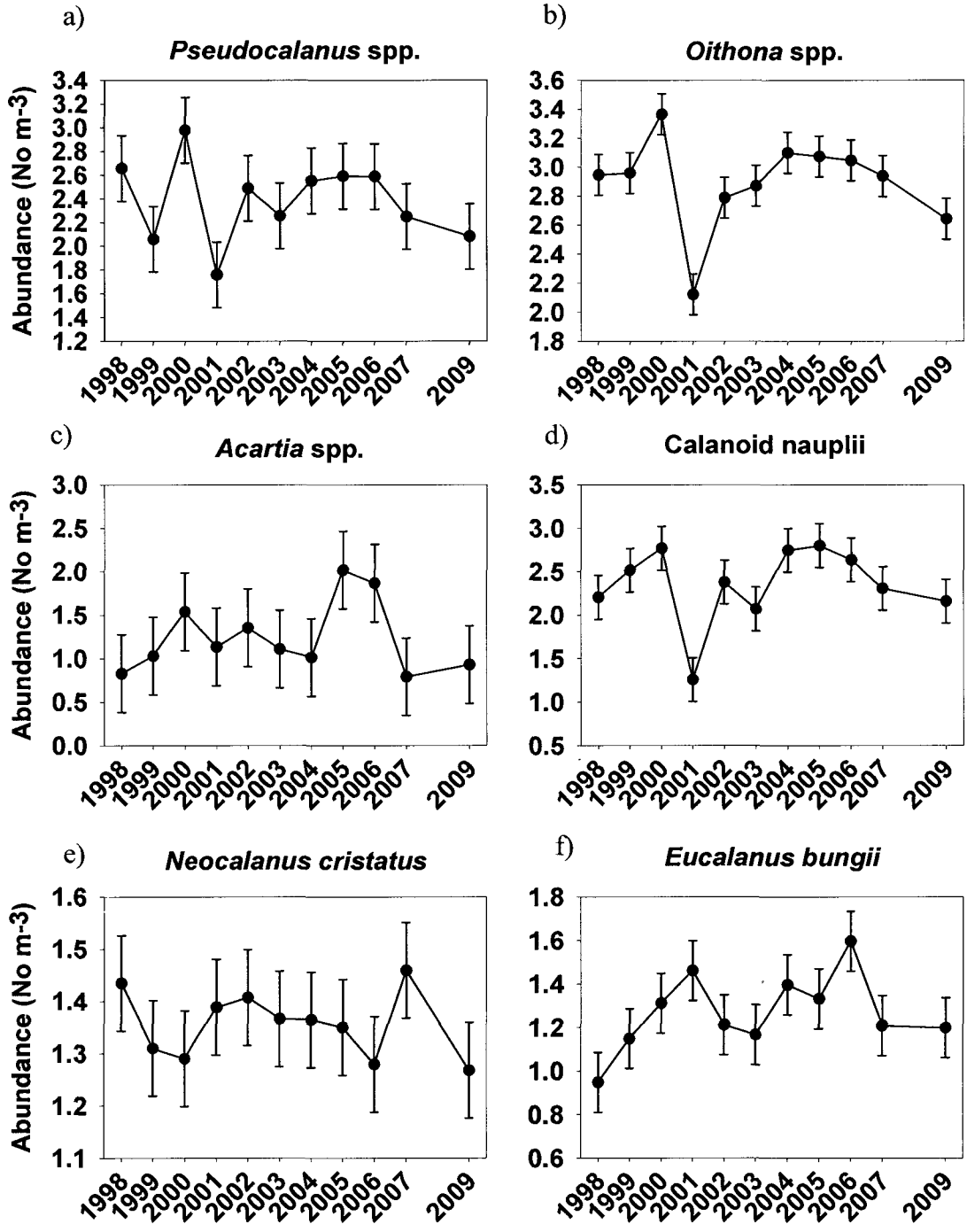


Figure 3.4. Annual changes in major zooplankton taxa mean abundance in May along the Seward line in the northern GOA 1998-2009; error bars are 95% confidence intervals

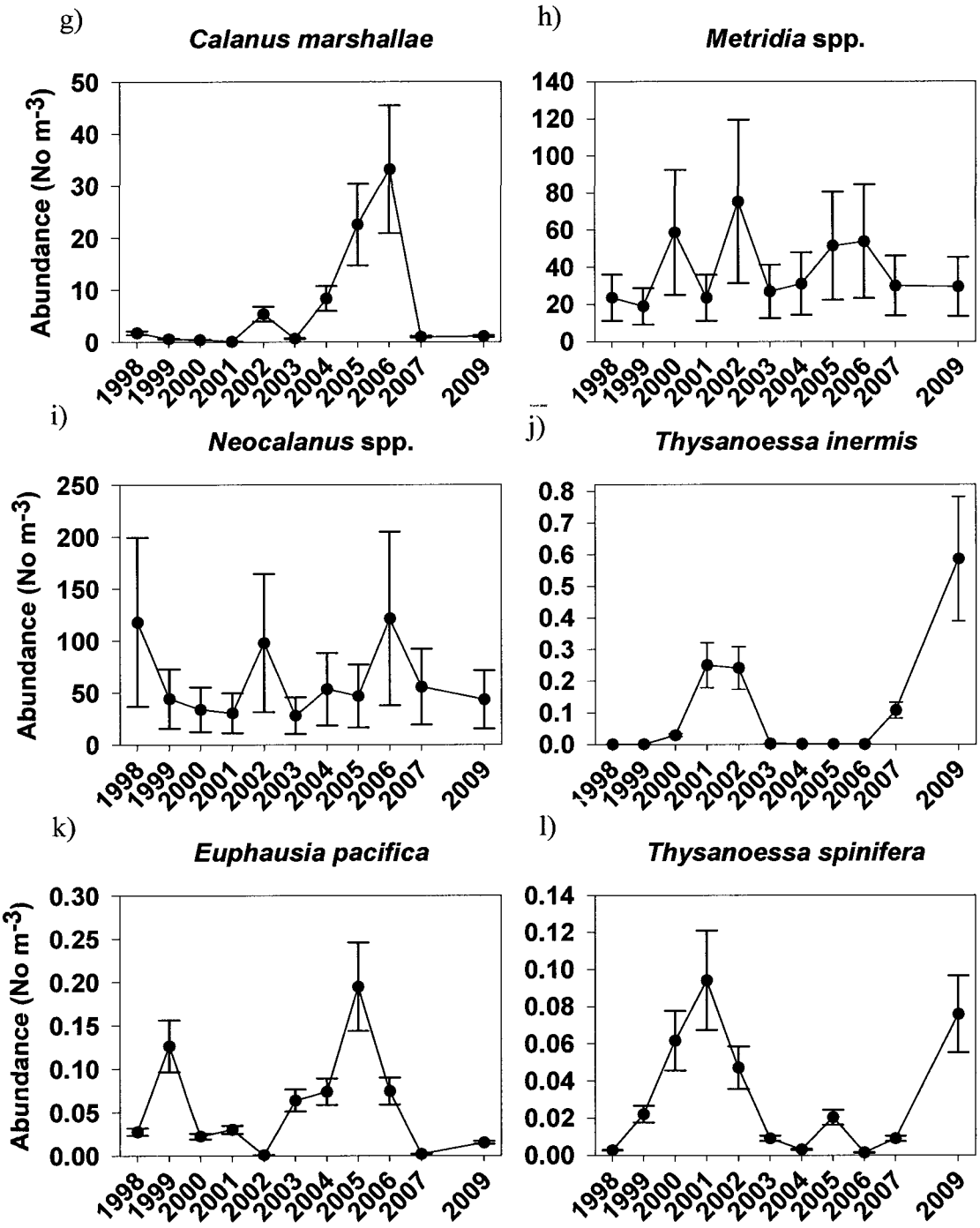


Figure 3.4. Continued

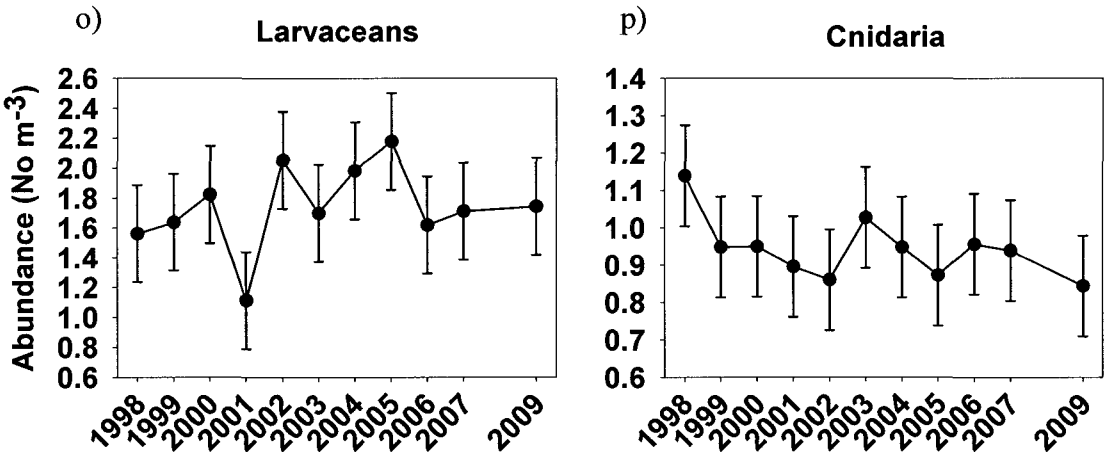
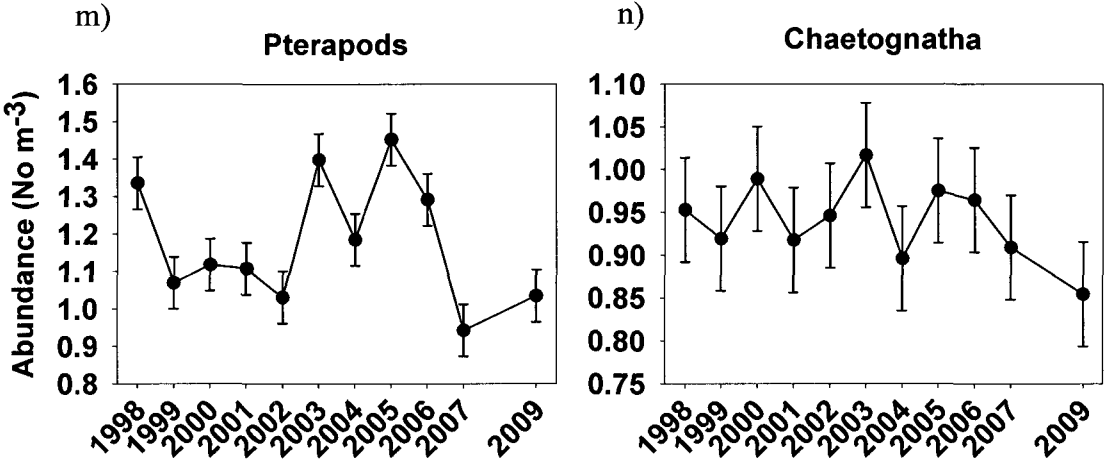


Figure 3.4. Continued


m)
Pterapods
Abundance (No m-3)
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2009
n)
Chaetognatha
1.10
1.05
1.00
0.95
0.90
0.85
0.80
0.75
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2009

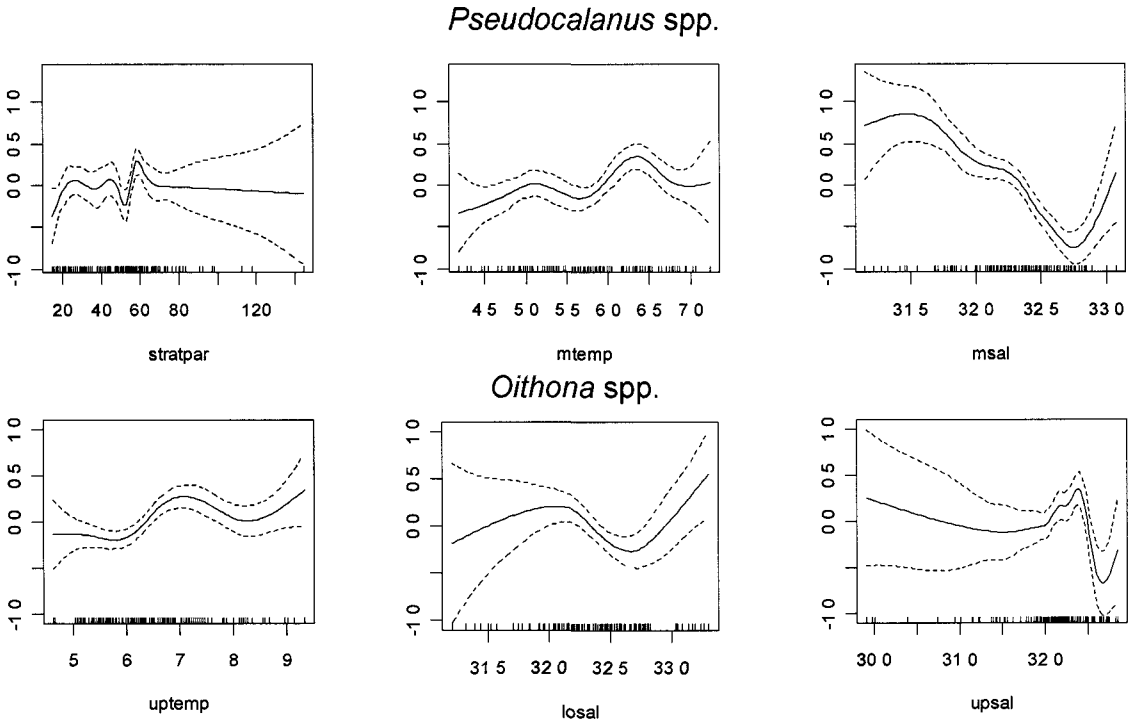


Figure 3.5. GAM best-fit models for *Pseudocalanus* spp., *Oithona* spp., showing fitted relationships and additive effects of significant water mass properties on zooplankton abundance in May along the Seward line in the northern GOA 1998-2009. Dashed lines: upper and lower pointwise twice-standard-error curves, zero on y-axis corresponds to no effect of relevant explanatory variable on zooplankton abundance; ticks along the x-axis: locations of data points along x-axis. For specific names see Table 3.3

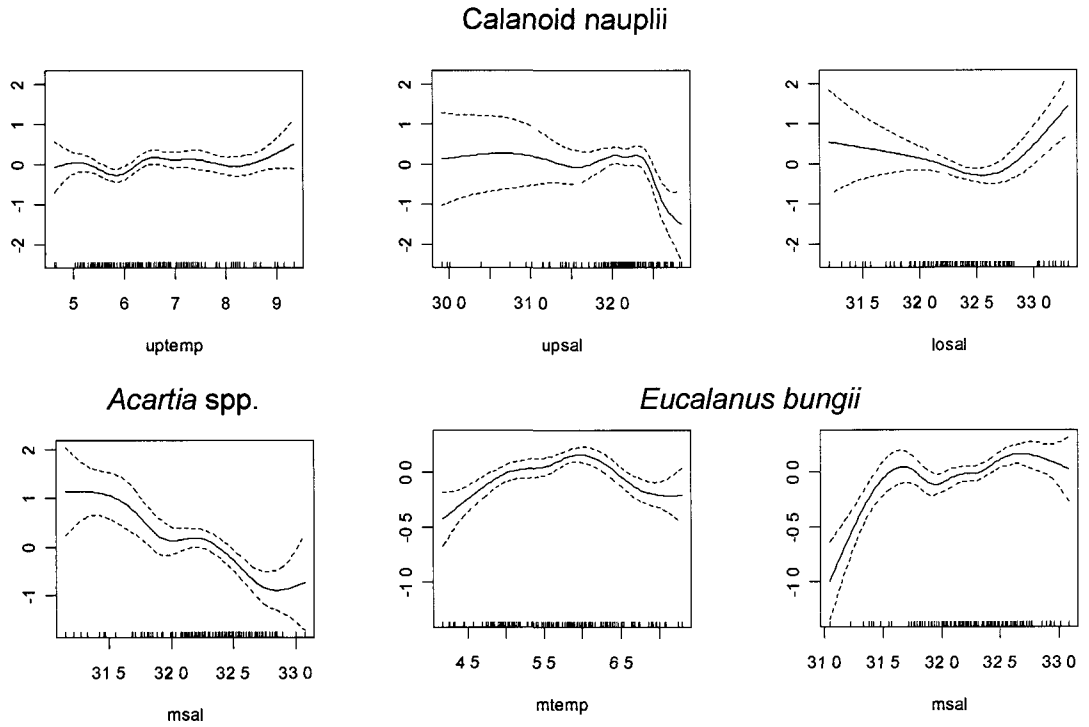


Figure 3.6. GAM best-fit models for calanoid nauplii, *Acartia* spp., *Eucalanus bungii*, showing fitted relationships and additive effects of significant water mass properties on zooplankton abundance in May along the Seward line in the northern GOA 1998-2009. Dashed lines: upper and lower pointwise twice-standard-error curves, zero on y-axis corresponds to no effect of relevant explanatory variable on zooplankton abundance; ticks along the x-axis: locations of data points along x-axis. For specific names see Table 3.3

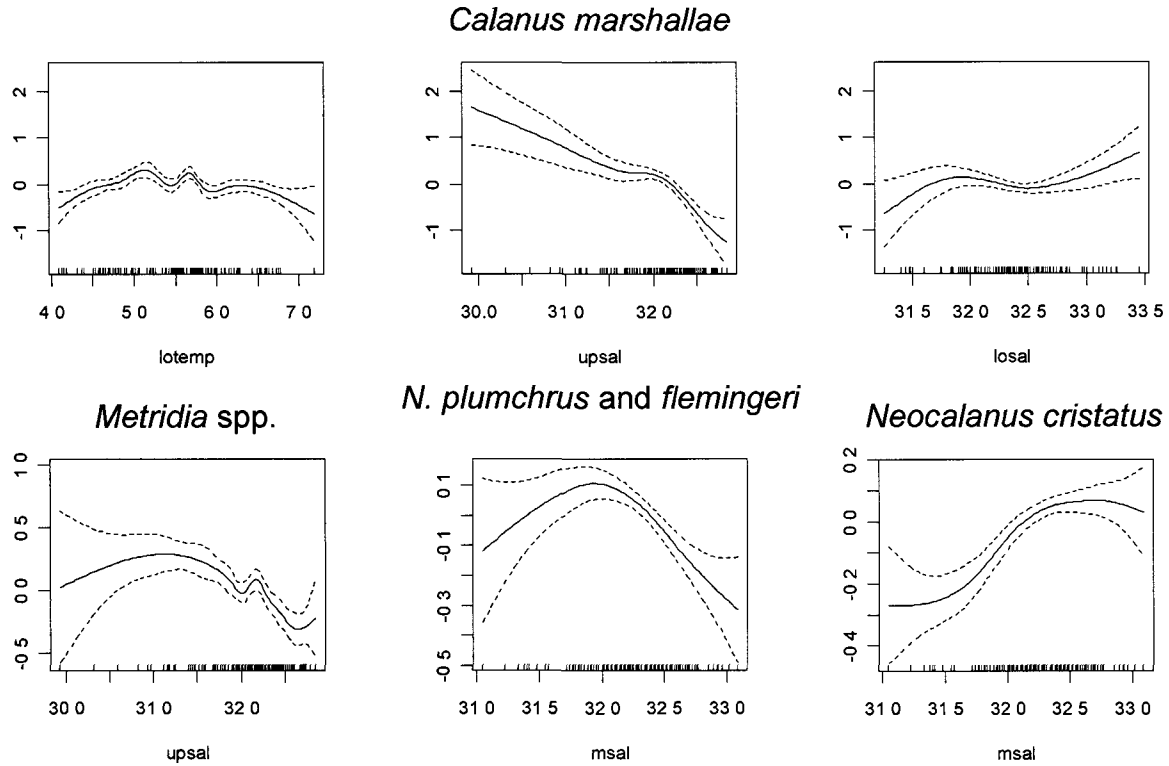


Figure 3.7. GAM best-fit models for *Calanus marshallae*, *Metridia* spp., *Neocalanus plumchrus/N. flemingeri*, *Neocalanus cristatus*, showing fitted relationships and additive effects of significant water mass properties on zooplankton abundance in May along the Seward line in the northern GOA 1998-2009. Dashed lines: upper and lower pointwise twice-standard-error curves, zero on y-axis corresponds to no effect of relevant explanatory variable on zooplankton abundance; ticks along the x-axis: locations of data points along x-axis. For specific names see Table 3.3

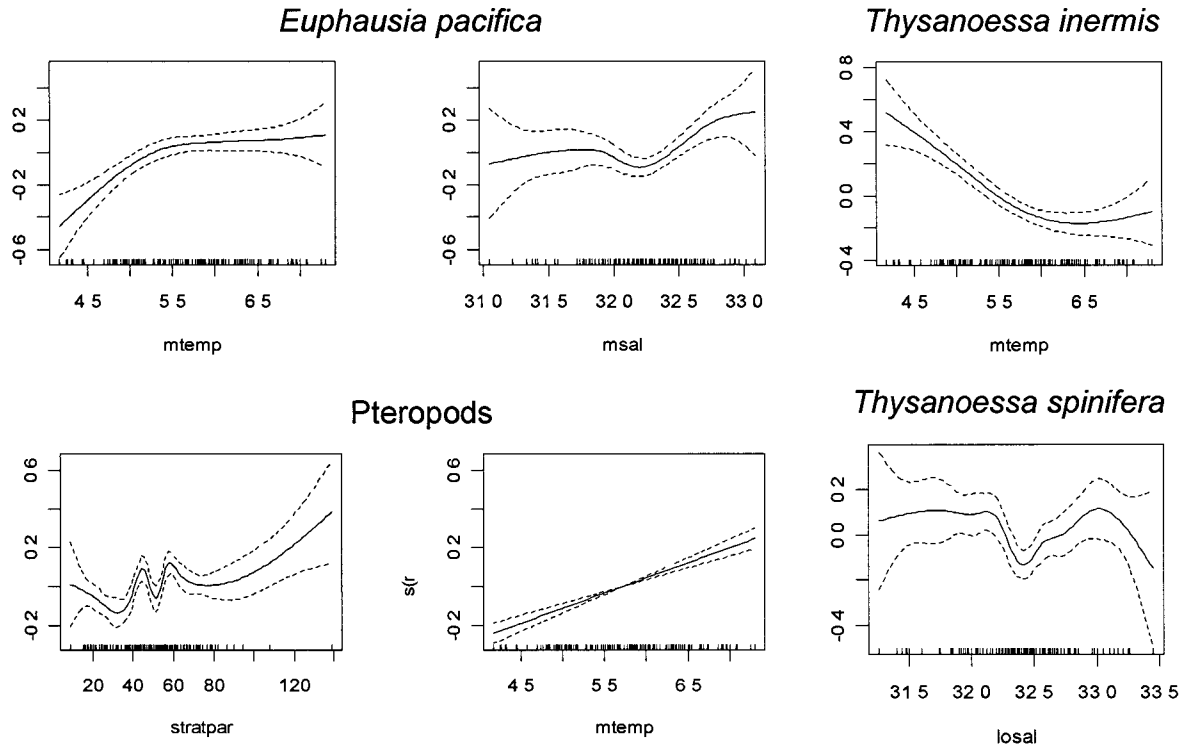


Figure 3.8. GAM best-fit models for *Euphausia pacifica*, *Thysanoessa inermis*, Pterapoda, *Thysanoessa spinifera*, showing fitted relationships and additive effects of significant water mass properties on zooplankton abundance in May along the Seward line in the northern GOA 1998-2009. Dashed lines: upper and lower pointwise twice-standard-error curves, zero on y-axis corresponds to no effect of relevant explanatory variable on zooplankton abundance; ticks along the x-axis: locations of data points along x-axis. For specific names see Table 3.3

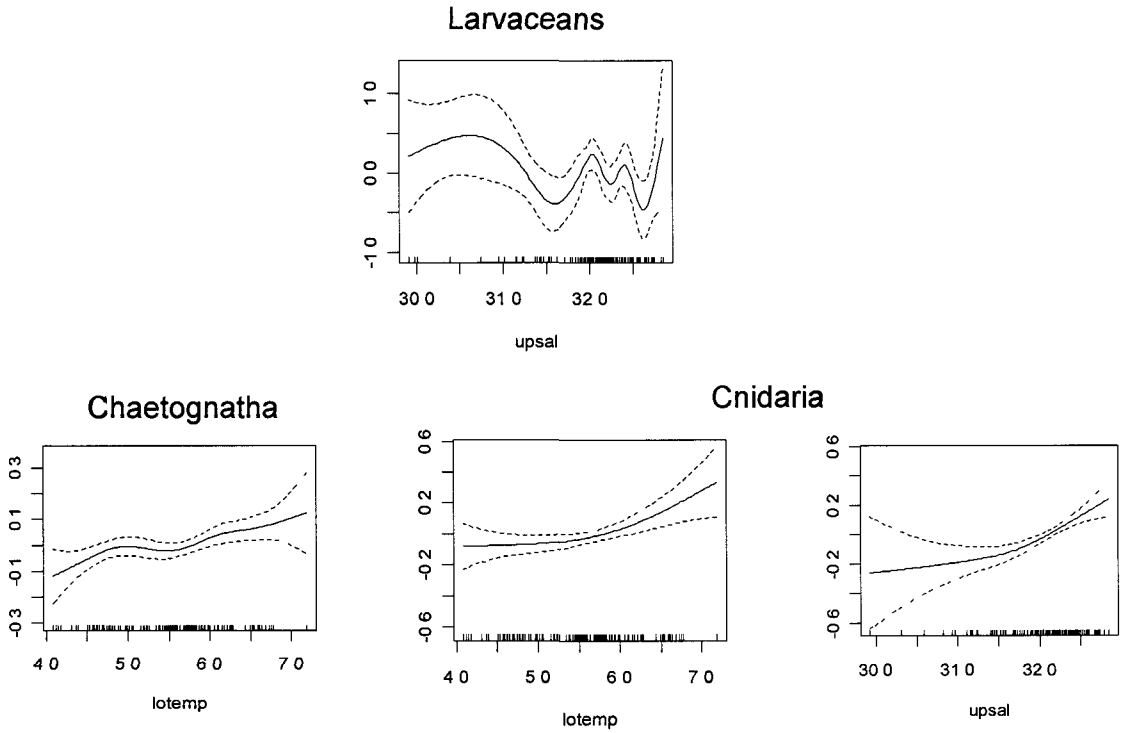


Figure 3.9. GAM best-fit models for Larvacea, Chatognatha and Cnidaria, showing fitted relationships and additive effects of significant water mass properties on zooplankton abundance in May along the Seward line in the northern GOA 1998-2009. Dashed lines: upper and lower pointwise twice-standard-error curves, zero on y-axis corresponds to no effect of relevant explanatory variable on zooplankton abundance; ticks along the x-axis: locations of data points along x-axis. For specific names see Table 3.3

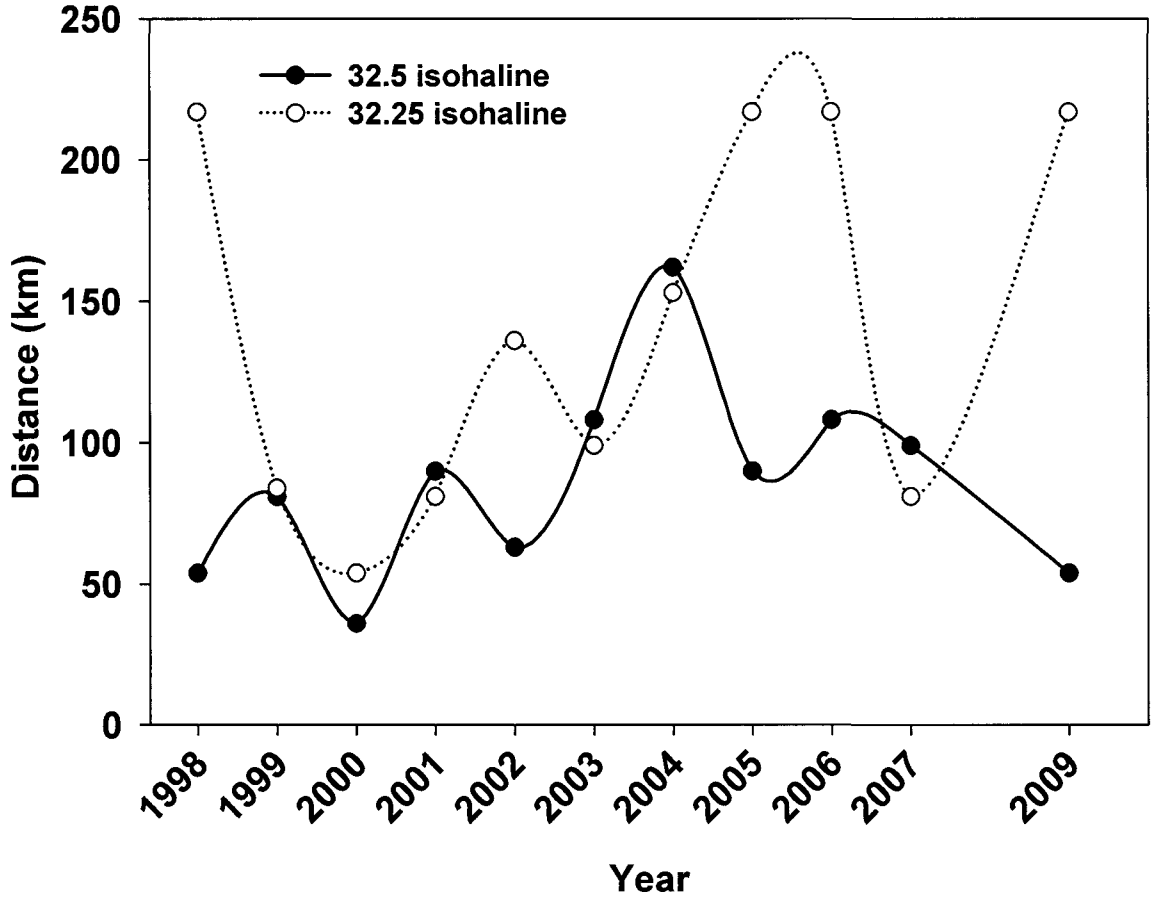


Figure 3.10. Farthest distance of 32.25 isohaline from shore at depths <100 m (white circles) and closest distance of the 32.50 isohaline to shore at depths < 100 m(black circles) by year along the Seward line in the northern GOA in May

CONCLUSIONS

Most of the literature on the distribution, abundance and feeding habits of seabirds indicates that high seabird densities are directly associated with high prey densities (Logerwell and Hargreaves 1996; Davoren et al. 2003; Ainley et al. 2005) or indirectly associated with increased primary and secondary productivity (Springer et al. 1996; Nel et al. 2001; Vilchis et al. 2006; Hyrenbach et al. 2007). However, the data presented in this study did not show an association in seabird abundance and secondary productivity as indicated by zooplankton biomass, despite the intense survey effort (580 h and 3004 km^2), temporal coverage (1998-2003; winter, spring, summer and fall), and sampling of physical (temperature, salinity, density, nutrients, satellite altimetry) and biological parameters (acoustics- 420 kHz, 200 kHz, 120 kHz and 38 kHz, and zooplankton – CalVET and MOCNESS, surface chlorophyll-SeaWiFS; and chlorophyll *a* concentration – upper 50 m) (several physical and biological parameters not included in this dissertation). I undertook an extensive analysis of these datasets to develop predictive models to identify spatio-temporal associations between seabirds and physical and biological parameters. However, extreme variability in the data precluded model development because algorithms that are intrinsic to model computation did not converge (Hollander and Wolfe 1999; Allison 2001; Wood 2006). High variability, zero-inflated and overdispersed data are common challenges when analyzing seabird abundance and distribution. Most studies are able to curtail those difficulties by using logarithmic transformations, negative binomial distributions, or "quasi" link functions for model

development (Ainley et al. 2005; Jahncke et al. 2005; Yen et al. 2005; Vilchis et al. 2006; Hyrenbach et al. 2007). However, these techniques did not work in this study, and statistical models did not converge (logistical and Poisson regressions, generalized additive models).

Most studies that have detected associations between seabirds and prey and their habitat at sea are constrained to the breeding season, proximity to shore and to regions of high biological productivity, such as the southeastern Bering Sea, Bering-Chukchi shelf, Aleutian Island passes, Antarctica, and upwelling systems (Veit et al. 1993; Hunt et al. 1996; Logerwell and Hargreaves 1996; Springer et al. 1996; Davoren et al. 2003; Hyrenbach and Veit 2003; Ainley et al. 2005; Jahncke et al. 2005; Yen et al. 2005; Garthe et al. 2007). In areas where biological productivity is not as high and seabird abundances are low, it seems necessary to greatly extend spatio-temporal coverage of the study in order to detect associations among seabird and prey and their habitat (Spear et al. 2001 - 10 years, 7,196 km^2; Vilchis et al. 2006 - 18,848 km^2, Hyrenbach et al. 2007 – 14, 796 km^2). Furthermore, most studies that were able to develop predictive models between seabirds at sea and prey and their habitat used grid sampling design or multiple transects across the shore (Spear et al. 2001; Hyrenbach and Veit 2003; Ainley et al. 2005; Vilchis et al. 2006). Few studies have been successful in developing predictive models while using single transect surveys (Yen et al. 2005; Hyrenbach et al. 2007; Ribic et al. 2008), and the caveat in these studies was compensated by large-scale coverage (>1000 km) and season restriction (spring/summer; Yen et al. 2005). In some cases

statistical rigor was not applied and a mix of converging and non-converging models was used to compare species associations to habitat parameters (O'Hara et al. 2006).

The results and challenges encountered in this study resemble the ones by Fauchald et al. (2002), Burger (2003), and Grémillet et al. (2008). The study by Fauchald et al. (2002) used nine years of winter data (January-March) and covered 1000's of km of the Barents Sea and did not detect spatial predictability between seabird aggregations and oceanographic features that enhance the general density of potential prey. Fauchald et al. (2002) state that the use of restricted survey data may be misleading when extrapolating and predicting the distribution of seabirds. In the study by Burger (2003), extreme spatial and temporal variability in predictor and response variables precluded the development of predictive models. This was a small-scale study on the western coastal region of Vancouver Island, Canada; this region is subject to similar episodic eddy activity as the ones encountered in the present study in the northern GOA (Okkonen et al. 2003; Janout et al. 2009; Ladd et al. 2009). Small spatial coverage and high environmental variability were likely the main factors preventing the development of predictive models by Burger (2003). Grémillet et al. (2008) found a spatial mismatch between seabirds and fishes, zooplankton and fishes, and fisheries and fishes. This spatial mismatch occurred despite the spatial match between seabirds and chlorophyll, and seabirds and low sea-surface temperature, associated with the upwelling of the Benguela current system. These previous studies in conjunction with the present one highlight the difficulties of predicting the spatial distribution of seabirds.

The use of physical parameters (temperature and salinity) to predict changes in zooplankton distribution proved to be successful in this study. The large data set (10 years) and the susceptibility of zooplankton to ocean currents (Mann and Lazier 1996) and water mass properties contributed to this success.

Despite the challenges encountered the present study, there was an increase in knowledge regarding the habitat use of seabird foraging guilds, seasonal variations in seabird abundance, and changes in zooplankton abundance in relation to water mass properties. Overall abundance of seabirds did not follow seasonal changes in zooplankton biomass. Seabird abundance was low in the study area, when compared to other regions in the GOA. Furthermore, low bird densities suggest that productivity in this study area is not high enough to sustain a significant seasonal increase in local seabird abundance. In order to detect seasonal changes in seabird abundance and their potential prey in the northern GOA it is necessary to sample forage fish during spring, summer and fall periods. In addition, expanded grid sampling of along shore and cross shore transects should be used to better capture the spatial variations in seabird habitat use in this area.

Water mass properties and abundance of seabird foraging guilds were different across the shelf in the northern GOA. The high abundance of divers and surface feeders in conjunction with high total zooplankton biomass on the middle shelf suggests that this zone is an important habitat for both seabird foraging guilds. Murres (divers) were the most abundant seabird species during winter and early spring in the northern GOA and

they were positively associated with *Thysanoessa inermis* biomass and low-density waters. Northern fulmars were the most abundant surface feeders in this region and were positively correlated with warmer saline waters and Cephalopoda paralarvae biomass. The middle shelf can be characterized as a transition zone between neritic and oceanic environments. Large ranges in salinity and temperature across the shelf occurred between cruises and influenced the distribution of neritic and oceanic zooplankton along the Seward line. The northern GOA is an important wintering area for murres, which may rely on *Thysanoessa inermis* during March and April, prior to the increase in forage fish abundance in this region. More information on the seasonal distribution and abundance of forage fishes and Cephalopoda life stages are critical to improve the understanding of habitat use and prey selection by seabird foraging guilds in the northern GOA.

The northern GOA has undergone significant variations in temperature, salinity and zooplankton abundance in May from 1998-2009. The data indicate that very few species in the zooplankton community are able to maintain high abundances when water temperatures are high and there is an early and weak phytoplankton spring bloom. Furthermore, neritic species that depend on lipid reserves to overwinter (i.e.: *Thysanoessa inermis*, *Calanus marshallae*) may undergo extreme declines in abundance if these conditions are preceded by warm winters. Species that are able to feed on a wide range of particle sizes (*Pseudocalanus* spp., *Neocalanus plumchrus/N. flemingeri*, *Euphausia pacifica*) and those that have a flexible diet (*Oithona* spp.) appeared to be

more resilient to warmer conditions than *T. inermis* and *C. marshallae*. Perhaps these species are more resilient due to a combination of different factors such as lower metabolic rates (*Euphausia pacifica*), different life history strategies (*Pseudocalanus* spp. and *Oithona* spp.) and overwintering depth distribution (*N. plumchrus/N. flemingeri*) (Saito and Tsuda 2000; Lischka and Hagen 2007; Pinchuk et al 2008). High zooplankton abundances in years of substantial cross-shelf mixing suggest that iron and nutrient transport between the shelf and oceanic domains that create high phytoplankton biomass are essential for sustaining high copepod populations. The abundance of zooplankton in the northern GOA is highly influenced by advective processes and changes in temperature. Their complex life histories, vertical distribution patterns and habitat associations have a major influence on the response of each taxon to changes in environmental conditions. Further understanding of biological and physical mechanisms that control the GOA ecosystem are of major importance to predict the response of zooplankton communities to environmental changes.

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Appendix 1. Description of the observation conditions data, entered at the beginning of each count interval (5 min), during bird surveys conducted along the Seward line in the northern GOA from 2000-2003; Beaufort Scale and description according to wind speed (knots) and wave height (m) (a), and observation conditions (b)

a)

Beaufort Scale	Wind Speed	Wave Height	Description
0	0-1	0.0	Calm - sea smooth and mirror-like
1	2-3	0.1	Light air - scale-like ripples without wave crests
2	4-6	0.2	Light breeze - small, short wavelets; crests have a glassy appearance and do not break
3	7-10	0.6	Gentle breeze - large wavelets; some crests begin to break, but foam is glassy, occasional white caps
4	11-16	1.2	Moderate breeze - small waves that become longer; fairly frequent whitecaps
5	17-21	1.8	Fresh breeze - moderate waves taking a more pronounced long form; many whitecaps; there also may be some spray
6	22-27	3.0	Strong breeze - large waves begin to form; whitecaps are extensive and everywhere, some spray
7	28-33	4.3	Near gale - sea heaps up and white foam from breaking waves begins to be blown in streaks along the direction of the wind, spin drift begins

Appendix 1. Continued

b)

Observation Conditions	Description
1	Poor
2	Fair
3	Good/Moderate
4	Very Good
5	Excellent

Appendix 2. Family, species, common name and count of all birds that occurred along the Seward line during all cruises from 1997-2003 in the northern GOA

Family and Species	Common Name	Bird Count
Gaviidae		
Gavia spp.	unidentified loon	7
Gavia pacifica	pacific loon	36
Gavia stellata	red-throated loon	6
Diomedeidae		
Phoebastria albatrus	short-tailed albatross	2
Phoebastria nigripes	black-footed albatross	643
Phoebastria immutabilis	Laysan albatross	184
Procellariidae		
Fulmarus glacialis	northern fulmar	3485
Puffinus spp.	dark shearwater	664
Puffinus bulleri	Buller's shearwater	9
Puffinus griseus	sooty shearwater	364
Puffinus tenuirostris	short-tailed shearwater	36
Pterodroma inexpectata	mottled petrel	22
Oceanitidae		
Oceanodroma spp.	unidentified storm-petrel	30
Oceanodroma furcata	fork-tailed storm-petrel	4727
Oceanodroma leucorhoa	Leach's storm-petrel	270

Appendix 2. Continued

Family and Species	Common Name	Bird Count
Phalacrocoracidae		
Phalacrocorax spp.	Unidentified cormorant	17
Phalacrocorax auritus	double-crested cormorant	170
Phalacrocorax penicillatus	Brandt's cormorant	5
Phalacrocorax pelagicus	pelagic cormorant	29
Anatidae		
Branta canadensis	Canada goose	11
Branta bernicla	brant	162
Anas platyrhynchos	mallard	1
Anas acuta	northern pintail	6
Anas clypeata	northern shoveler	7
Aythya marila	greater scaup	26
Somateria mollissima	common eider	29
Melanitta fusca	white-winged scoter	52
Phalaropodidae		
Phalaropus spp.	unidentified pharalope	48
Phalaropus fulicaria	red phalarope	329
Phalaropus lobatus	red-necked pharalope	7

Appendix 2. Continued

Family and Species	Common Name	Bird Count
Stercorariidae		
Stercorarius spp.	unidentified jaeger	8
Stercorarius pomarinus	pomarine jaeger	48
Stercorarius parasiticus	parasitic jaeger	9
Stercorarius longicaudus	long-tailed jaeger	4
Laridae		
Larus spp.	unidentified gull	34
Larus hyperboreus	glaucous gull	20
Larus glaucescens	glaucous-winged gull	573
Larus argentatus	herring gull	42
Larus canus	mew gull	27
Larus philadelphia	Bonaparte's gull	5
Larus sabini	Sabine's gull	2
Rissa tridactyla	black-legged kittiwake	970
Sterna paradisaea	Arctic tern	89
Sterna aleutica	Aleutian tern	2
Alcidae		
Uria spp.	unidentified murre	325
Uria aalge	common murre	3029
Uria lomvia	thick-billed murre	41
Cepphus columba	pigeon guillemot	7

Appendix 2. Continued

Family and Species	Common Name	Bird Count
Alcidae (continued)		
Brachyramphus spp.	unidentified murrelet	124
Brachyramphus marmoratus	marbled murrelet	102
Brachyramphus brevirostris	Kittlitz's murrelet	88
Synthliboramphus antiquus	ancient murrelet	108
Ptychoramphus aleuticus	Cassin's Auklet	25
Aethia psittacula	parakeet auklet	13
Aethia spp.	unidentified auklet	34
Aethia cristatella	crested auklet	8
Aethia pusilla	least auklet	2
Cerorhinca monocerata	rhinoceros auklet	15
Fratercula corniculata	horned puffin	108
Fratercula cirrhata	tufted puffin	1569
TOTAL		**18,815**